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STUDIES ON THE BIOLOGY OF MANCOCUMA STELLIFERA ZIMMER, 1943 (CRUSTACEA: CUMACEA)

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STUDIES ON THE BIOLOGY OF *MANCOCUMA STELLIFERA* ZIMMER, 1943 (CRUSTACEA: CUMACEA)

by

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A THESIS

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ABSTRACT

The cumacean Mancocuma stellifera Zimmer, 1943 is redescribed and figures of the species are presented for the first time. This thesis constitutes the first report of the species from the continental United States, and its known geographical range is reported from the Gulf of St. Lawrence to Cape Ann, Massachusetts. These data indicate that the species should be included with the western Atlantic boreal fauna, and as a member of the infauna of nearshore subtidal sands.

Quantitative studies were made of seasonal reproductive biology, zonation and density variations of a population of M. stellifera at Jenness Beach, Rye Beach, N. H., from 1968 to 1969. Annual breeding cycles commenced in spring and peaked in late summer, when water temperatures were about 4° and 16° C, respectively. Two distinct generations were produced annually, in mid-summer and early fall. Sex ratios approaching 1:1 occurred only during spring and summer breeding periods. Females produced two or more broods annually, estimated incubation periods were one month in summer and two months in winter, and estimated maximum life spans were 7 months for males and 11 months for females.

Seasonal subtidal transects employing an Ekman dredge showed that M. stellifera inhabited subtidal sands at water depths of 0 - 7 m below low water levels, and that the main segment of the population occurred at water depths of 1 - 5 m, where mean sand grain diameters ranged from 0.385 to 0.166 mm,

respectively. Similar results were obtained for subtidal transects at Wallis Sands Beach, Rye Beach, N. H., and Long Sands, York Beach, Me. The Jenness Beach population did not occur on air-exposed sands or migrate onto intertidal sands on flooding tides. No significant differences in zonation occurred by season or sexes, although small juveniles and manca larvae comprised 73 - 95% of the population at water depths of 5 - 7 m during reproductive periods. Habitat mean densities ranged from a maximum of 312.1/0.023 m^2 in fall to a minimum of 69.6/0.023 m^2 in spring. It was concluded that the Jenness Beach population functioned as an ecological unit including all life history stages. Extrapolation of the maximum density obtained for the species at Jenness Beach gave a theoretical density estimate of 39,868/1.0 m^2, a value unsurpassed in the literature for Cumacea.

Reproductive, swimming, burrowing and feeding behavior were described. The precopula position was figured and considered as unique for Cumacea. Excised embryos were reared in the laboratory to the manca larval stage, and the manca larva was figured. Underwater observation and plankton sampling suggest that the species' tendency to swim is greatest during the manca larva stage, especially when brood releases coincide with new and full moons of lunar cycles. It was concluded that M. stellifera inhabits surface sands and does not burrow to depths greater than about 1 cm. Laboratory observations showed that M. stellifera is an epistrate feeder, and experimental evidence suggests that micro-organisms on sand grains constitute the species' primary food source.

Sand shrimp and flatfish preyed on M. stellifera under experimental conditions. Stomach analyses showed that flatfish and diving sea ducks preyed on other cumacean species at neighboring beaches and in the Great Bay estuary.

Salinity tolerance experiments of 5 to 20 °/oo were inconclusive, but the data suggest that M. stellifera is not particularly euryhaline.

Thirty-two species representing five phyla constituted the macrofaunal associates of M. stellifera at Jenness Beach at four seasonal subtidal transects. Crustaceans comprised over 90% of the fauna for every season, and of these, amphipods and cumaceans were the two most abundant orders. The amphipod Bathyporeia quoddyensis, and M. stellifera were the first and second numerically dominant species, respectively. It is proposed that nearshore subtidal sand associations of the western Atlantic boreal region, possessing physical and biological characteristics similar to Jenness Beach, be characterized as Bathyporeia - Mancocuma associations.

CHAPTER I

INTRODUCTION

The ecology of marine sand beaches and nearshore sand received relatively little attention prior to the 1950's (Hedgpeth, 1957), and, although investigations of this sometimes harsh and outwardly barren environment have increased during the last two decades, they were largely concerned with the intertidal zone. These studies show that the intertidal fauna are composed of relatively few, but often abundant species, and that crustaceans are the most universal of sand beach macrofauna (see Dahl, 1953; Colman and Seagrove, 1955; Hedgpeth, 1957; Bousfield, 1962b; Croker, 1967, 1970; Dexter, 1967, 1969; McIntyre, 1968, 1970; Fish, 1970; Fish and Preece, 1970 for many references). Benthic communities just seaward of the beach and surf line have, however, been virtually ignored until recent years. Investigations specifically concerned with sand bottom communities from 0 to 20 m below low water levels are few, but these data showed that crustaceans are again major components of the macrofauna (Holme, 1954; Barnard and Given, 1960; Barnard, 1963; Clutter, 1967; Edwards and Steele, 1968; Fager, 1968; Fager and Clutter, 1968; McIntyre and Eleftheriou, 1968; Fincham, 1969; Sameoto, 1969b; Corey, 1970; Day et al, 1971).

Ecological and systematic studies of intertidal sand macrofauna in the western Atlantic boreal region are few and mostly recent (Newcombe, 1935; Bousfield, 1962a, b, 1965; Sanders et al, 1962; Grant, 1965; Croker, unpublished), while

similar published studies on nearshore subtidal sand communities are restricted to Sameoto's (1969b) work on near shore sands of Barnstable Harbor, Mass. However, work in progress on near shore communities of Cape Cod Bay, by the Systematics-Ecology Program, Marine Biological Laboratory, Woods Hole, Mass. should provide important additions to knowledge.

Of the malacostracan crustacean orders represented in intertidal and subtidal sand communities, the Cumacea is one of the least studied, in spite of reports that cumaceans often constitute an important part of the subtidal infauna. Cumacea are entirely marine, cosmopolitan in distribution and members of soft bottom communities from 0 to 1100 m. The majority of the 770 species occur from 0 to 220 m (Jones, 1969). Jones (1963, 1969) compiled information on the biology, systematics and distribution of Cumacea, and his comprehensive references show that data on their ecology are scarce. In addition, the life histories of only four species have been worked out (Corey, 1969). In southern California, Barnard and Given (1960) found that cumaceans ranked third in abundance among Crustacea collected from 3 to 9 m, and Barnard (1963) reported that cumaceans were the most abundant and characteristic crustaceans collected from the surf zone to 10 m. Cumaceans ranked second to amphipods in numbers of species among shallow water Crustacea from the Washington coast (Lie, 1969), and densities of 100 to 200 cumaceans per 1/10 m^2 were reported from subtidal sands in Scotland (Corey, 1970). Cumaceans have also been reported from intertidal sands, but their numbers were few with occurrences generally limited to regions near low water levels (Foxon,

1936; Watkin, 1942; Dixon, 1944; Weiser, 1956, 1959; Pike and Le Sueur, 1958; Bousfield, 1962b; Croker, 1967; Morton and Miller, 1968; Dexter, 1969; Corey, 1970).

In the western Atlantic, the systematics and distribution of Cumacea are inadequately known (Smith, 1879; Calman, 1912; Stephensen, 1943), and reports on Cumacea of the Atlantic coast of North America in the past thirty-odd years are infrequent, ranging from Cape Breton Island to Georgia (Huntsman, 1923; Blake, 1929; Zimmer, 1943; Jones and Burbanck, 1959; Bousfield, 1962b; Croker, 1967; Dexter, 1969). During summer 1967, large populations of the cumacean, Mancocuma stellifera Zimmer, 1943 were found near low tide levels at Maine and New Hampshire beaches by Dr. Robert A. Croker and Mr. Stanley E. Blake (personal communication). Subsequent preliminary surveys made by myself at beaches in the vicinity of Portsmouth, New Hampshire, and of the Great Bay, New Hampshire, estuarine system indicated that M. stellifera inhabits coastal sands from low water levels to water depths of 3 to 4 m. Prior to this, M. stellifera was reported only from the Matamek River, Quebec, Canada (Zimmer, 1943) and the Bay of Fundy (Bousfield, 1962a).

During 1968-1970, over 50,000 M. stellifera were collected from Gulf of Maine nearshore sands in all seasons of the year. Comparisons of detailed studies of M. stellifera appendages and hundred of whole specimens belonging to both sexes and all age groups, with Zimmer (1943), revealed that the species was inadequately described. In addition, the original description lacked figures of the species, and it was based on only eleven ovigerous females and seven mature males.

I have therefore first redescribed M. stellifera, and have included complete figures for the species. The majority of the thesis contributes to our knowledge of the biology of this cumacean species, and to the ecology of nearshore sand bottom communities of the western Atlantic boreal region.

CHAPTER II

MATERIALS AND METHODS

1. Description of the Study Area.

Jenness Beach, Rye Beach, New Hampshire (Figs. 1 and 2) was selected as the study area for this investigation because it appeared to be a representative M. stellifera habitat. The beach is easily accessible throughout the year, within reasonable proximity to laboratory facilities, and small boats can also be launched directly from the beach without difficulty. The beach runs in a nearly straight northeast-southwest direction for 1.3 miles, curving slightly seaward where it joins bedrock headlands, Straw Point on the north and Rye Ledge on the south. The beach is technically classified as a baymouth bar, since beach building has cut off a marsh and lagoon (Eel Pond) from the sea (Tuttle, 1960). The beach had a slope of 2.69 degrees when surveyed in summer 1969, and hydrographic charts, my soundings and underwater observations show that this gentle slope continues subtidally, where the smooth sandy bottom is interrupted with occasional boulder pavements. Intertidally, the sediment is composed of cobbles at both ends, with rapid gradation into clean compact sand toward the center of the beach. Tuttle (1960) reported a median diameter of 0.17 mm for intertidal sand at Jenness Beach.

Jenness Beach is subject to semidiurnal tides with a mean range of 8.7 ft (Dr. Robert Croker, personal communication), and, by virtue of its alignment along the coast, to the fetch of storms generated from the easterly quadrant.

McIntire and Morgan (1964) reported that the annual storm period along the New England coast from Kennebunk Beach, Maine to Cape Ann, Massachusetts, reaches its peak during the winter months, November through March, with the majority of the gales coming from the east. Jenness Beach is, however, more protected from the effects of these easterly storms than its degree of exposure to the open sea would indicate. Offshore ledges and boulder pavements prevent high storm ridges from forming, and bedrock headlands dissipate wave energy by refraction (Tuttle, 1960). Also, the New Hampshire coastline is protected from the full force of southeasterly storms by Cape Ann (McIntire and Morgan, 1964). Jenness Beach's gentle slope and fine sand indicates that it more closely fits the description of a moderately protected beach, since exposed beaches have more severe slopes and coarser sands (Hedgpeth, 1957; Bascom, 1960; Strahler, 1966; Bird, 1968; Morton and Miller, 1968).

The Jenness Beach population of M. stellifera was studied and sampled throughout the period of this investigation, July 1968 through August 1970. All laboratory and field methods described below apply to this population, unless otherwise noted.

Figure 1. Map of the New Hampshire and southern Maine coasts showing locations of the study area and sampling stations. 1, Jenness Beach; 2, Wallis Sands; 3, Little Harbor; 4, Dover Point; 5, Long Sands.

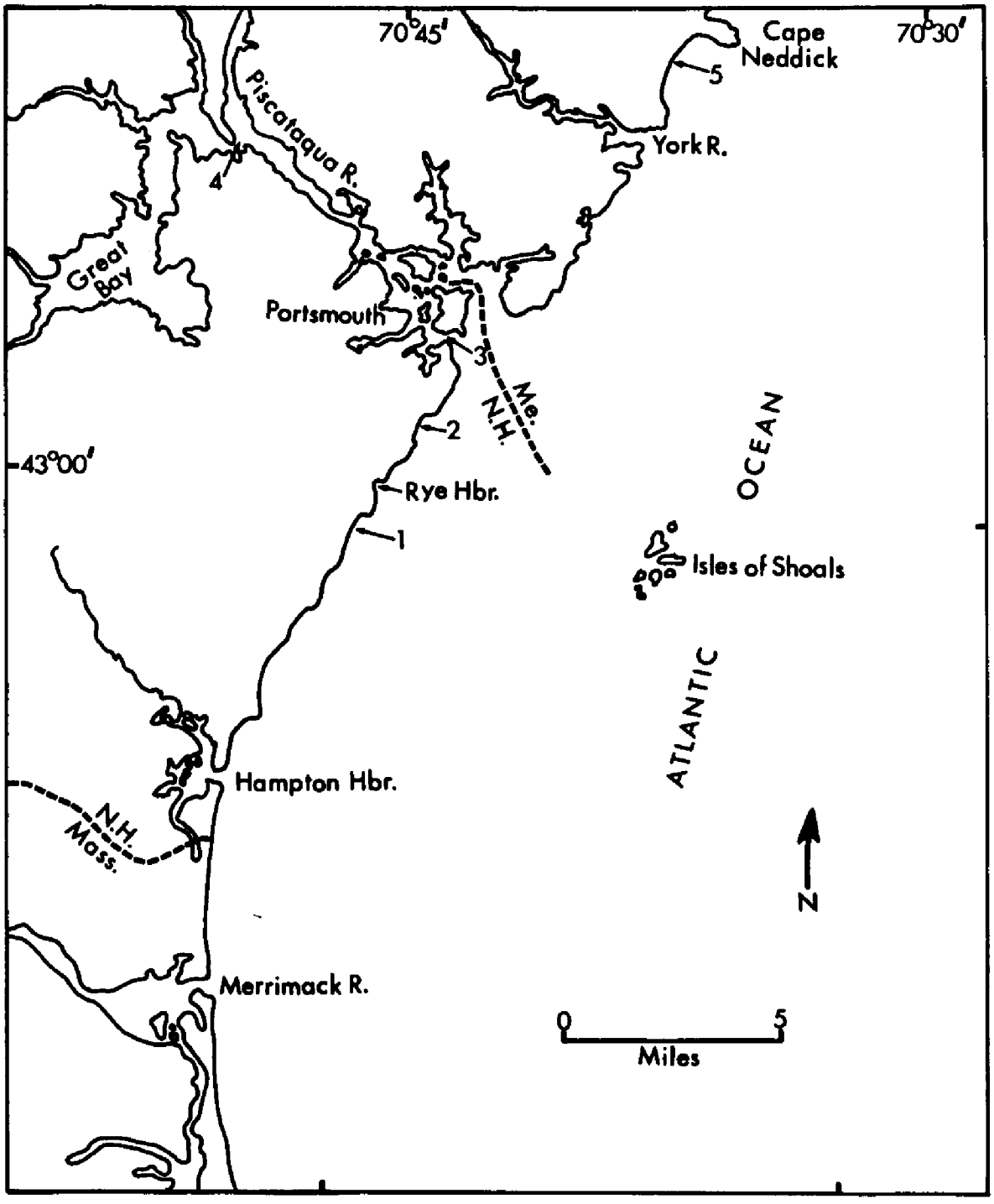
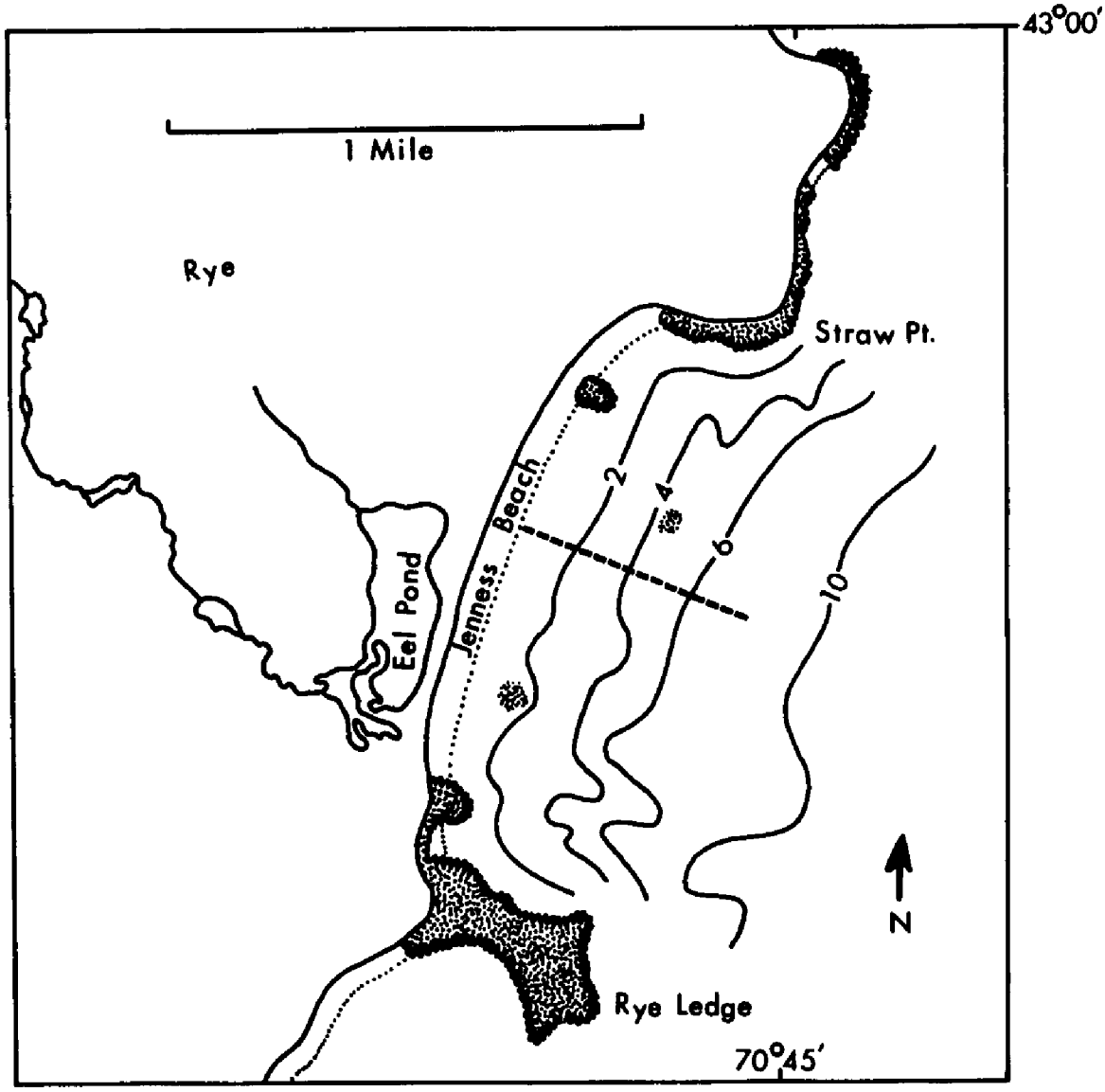

70°45'
70°30'
Cape Neddick
5
York R.
Piscataqua R.
4
Great Bay
Portsmouth
3
Me.
N.H.
2
43°00'
Rye Hbr.
1
OCEAN
Isles of Shoals
ATLANTIC
Hampton Hbr.
N.H.
Mass.
N
Merrimack R.
0
5
Miles

Figure 2. Map of Jenness Beach. Stippled areas, bed rock and boulder pavements. Broken line, location of subtidal transects and SCUBA observations. Dotted line, mean high water. Isobaths in meters.


43°00'
1 Mile
Rye
Straw Pt.
Jenness Beach
2
4
6
10
Eel Pond
N
Rye Ledge
70°45'

2. Field Studies

Population Aspects.

Data on reproductive cycles, sex ratios, fecundity and population composition were obtained by taking a set of 5 to 10 samples monthly with an Ekman dredge 15 cm on a side at water depths ranging from 0.5 to 1.0 m below the low water level on the day of sampling. This yielded a sample of 0.023 m^2 area. Samples could not always be taken at exact thirty day intervals, since sea conditions dictated when this work could be accomplished. Each set was taken on the same day, and only when the sea was calm. Samples were taken by wading into the water and placing the dredge on the bottom, in an open position and at arm's length from the body, only where the sand had not been disturbed by walking movements or by a breaking wave. After the dredge was closed, its contents were emptied into a plastic tray supported by a float which was held in position by a five lb mushroom anchor. The tray was then carried to shore and the sample was transferred to a plastic bag for temporary storage. A full neoprene rubber wet suit was worn for sampling in colder months.

Separation of animals from the sediment was accomplished by washing each sample through a circular metal sieve measuring 20 cm in diameter, 5 cm deep and with a mesh size of 0.25 mm^2. Preliminary analyses showed that this mesh retained the smallest specimens of M. stellifera (manca larva), and even smaller faunal associates, while all but a fraction of the total sediment passed through. Following each separation, sieve

contents were transferred to permanent storage jars and preserved in 5% neutral buffered formalin.

Each monthly set of samples was treated in the following ways. Sex ratios and reproductive cycles for M. stellifera were determined by counting the total numbers of mature females, mature males and immatures in all samples. These counts were expressed as per cent frequencies for each category.

Monthly size classes for M. stellifera were estimated by measuring body lengths of the following stages:

mature female - marsupium fully developed; with or without a brood.

mature male - pleopods and second antennae completely developed.

maturing female - oostegites not completely developed; with ripening ovaries and vestigial fourth thoracic exopodite.

maturing male - pleopods and second antennae not completely developed, and with the fourth thoracic exopodite partially or completely developed.

juvenile - unsexable.

Length is defined as the distance from the anterior margin of the carapace to the tip of pleon somite 6, when the animal was stretched out. Measurements of fully extended animals were made to the nearest 0.04 mm under a binocular microscope incorporating an ocular micrometer. When large numbers of animals were available, subsamples of 150 were measured for each category; if animals in each category numbered fewer than

150, all were measured. Per cent frequencies were calculated and length frequency histograms were constructed for each of the stages.

Subsamples of mature, ovigerous females were used to obtain data on fecundity for each month. Fecundity is defined as the number of embryos present in the marsupium. If more than fifty females were available, the subsample size was fifty. Otherwise, the brood size was counted for all females. Only females with intact broods were used, and embryos were removed under a dissecting microscope using a pair of watchmaker's forceps and a small dissecting needle. Fecundity was expressed as the mean number of embryos per female per month, and the standard deviation was calculated for each mean. The stage of development of each brood was determined and females were measured to the nearest 0.04 mm in the way previously described.

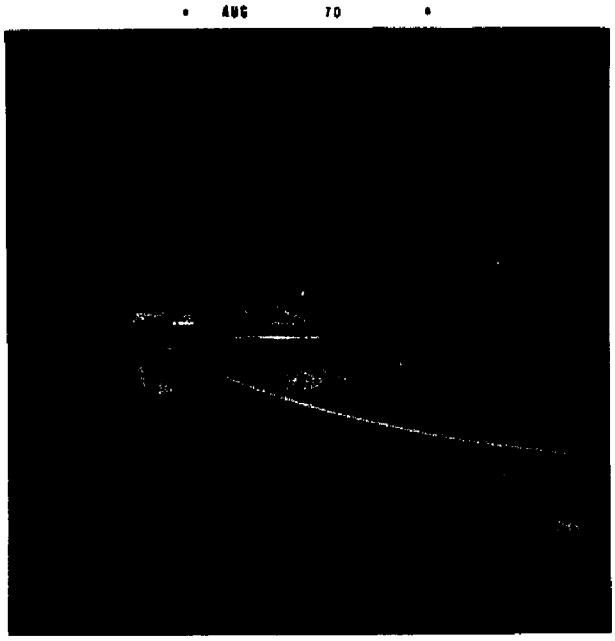
Seasonal subtidal transects were made at Jenness Beach from the low water levels on the day of sampling to a water depth of 7 m to provide data on population densities and bathymetric zonation. A 15 ft dory, equipped for beach launching, was used to obtain samples from water depths greater than 1 m. The dory was ideally suited for field work of this nature. It was small enough for cartop transportation, and its light plywood construction enabled one to handle it with ease. In addition, it was extremely seaworthy, and its design ensured safe traverse of the surf zone. The entire transect sampling procedure was reduced to a one-man operation after

a two-wheeled dolly, constructed from bicycle wheels, was assembled for transporting the dory across intertidal sands (Fig. 3). Low water and 1 m samples were taken by wading in the way previously described. A transect was established by placing one gallon bottles, tethered to a brick anchor by a measured 1/16 in nylon line, in a straight line perpendicular to the beach, at 1 m water depth intervals. Ekman dredge samples were taken in duplicate, 30 ft apart (two dory lengths), at each station along the transect to give a set of sixteen samples per transect. When samples were taken from the dory, a line was attached to the dredge and a messenger was used to trip the closing mechanism. Dory dredge samples were retrieved by first transferring the contents of the dredge to a plastic tray supported by a float secured to the side of the boat. This minimized the loss of dredge contents by leakage. The tray contents were then temporarily stored on board the boat in plastic bags. The total elapsed time required to complete a transect was approximately one hour, i.e., one-half hour before and after the tide reached predicted low water level.

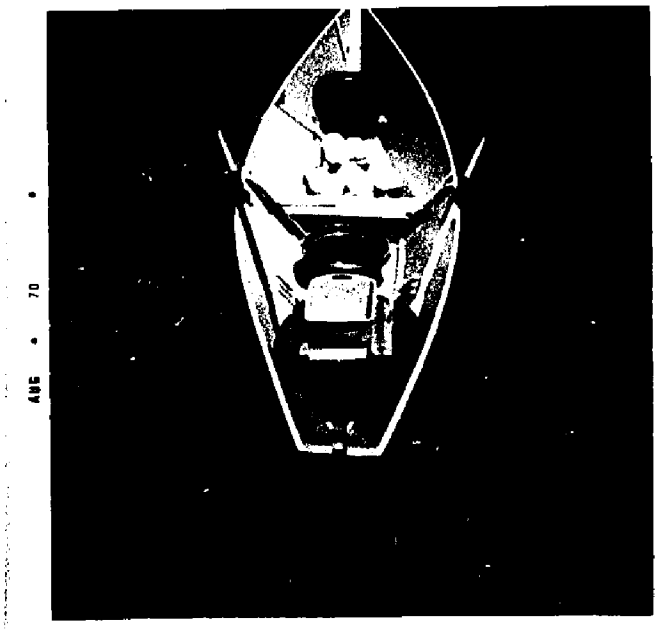
Two similar subtidal transects were made at Wallis Sands Beach, Rye Beach, N. H. in summer 1969, and at Long Sands Beach, York, Maine in summer 1970 (Fig. 1).

Two transects were made while Jenness Beach was covered with water at the time of high tide in summer 1969. They differed from the method described above only by running the transect from the high water level on the day of sampling to a water depth of 5 m.

Figure 3. Two views of the dory used for running subtidal transects. A - side view, showing two-wheel dolly for transporting the dory along the beach. B - interior view, showing stowage of collecting equipment.



A



B

Two intertidal transects were made in summer 1969. Both were made when the sand was exposed to the air, from the estimated high water level to the low water level on the day of sampling. Duplicate Ekman dredge samples, 2 cm deep and 15 m apart, were taken at 30 m intervals along the transect to give a set of twelve samples per transect.

All transect samples were separated in the way described for monthly samples. Faunal components were preserved in 5% neutral buffered formalin, and entire sediment volumes were retained for granulometric analysis, as follows: each sample was rinsed in fresh water, dried at room temperature and then passed through a series of sieves 3.36, 2.38, 1.00, 0.50, 0.25 and 0.125 mm. The arithmetic mean diameters of sand grains were calculated according to Krumbein and Pettijohn (1938).

Data on physical parameters, in addition to granulometry, were obtained by taking surface water temperature readings with a mercury thermometer and surface water salinity measurements with hydrometers at the time of sampling.

Density estimates were determined by counting total numbers of M. stellifera for all seasonal low water and high water transects at Jenness Beach, and for low water transects at Wallis Sands and Long Sands, and expressing their densities as mean numbers per 0.023 m^2 for each depth. Mean densities were calculated for M. stellifera faunal associate species for Jenness Beach low water subtidal transects only. Mean densities for each species for a particular transect were calculated on the basis of only those depths where each species was actually collected. These seasonal data were also used to

calculate sampling variances, standard errors and 95% confidence limits for M. stellifera for all Jenness Beach, Wallis Sands and Long Sands low water subtidal transects.

Plankton Sampling.

Plankton samples were taken periodically to determine if a pelagic stage exists at any time in the life history of M. stellifera. Three locations were sampled (Fig. 1): Little Harbor, New Castle, N. H.; Dover Point, Newington, N. H.; and Jenness Beach. Little Harbor faces the open ocean, is bordered by coastal beaches and is subject to strong tidal currents. Dover Point, at the mouth of the Little Bay-Great Bay estuarine system, is also subject to strong tidal currents from ocean water entering by way of the Piscataqua River. Ten minute night and day surface tows were made from a bridge spanning Little Harbor, and ten minute day surface tows were made with a boat at Dover Point, with a net measuring 50 cm across the mouth and with a mesh size of 0.5 mm.

Jenness Beach samples were taken with a No. 6 (standard silk bolting cloth) net measuring 30 cm across the mouth. Ten minute tows were made while wading in chest deep water under a variety of conditions: at time of high and low tides, on flooding and ebbing tides, during the day, on moonless and moonlit nights and during all but very strong surf conditions. The net was attached by its bridle to one end of a 4 ft wooden pole. The pole was held at a right angle to the body and the net was towed just beneath the surface. This technique reduced the probability of capturing animals forced into the water column by walking movements, or by contact of the net with the bottom.

Each plankton sample was analyzed in the following ways. Mancocuma stellifera was separated from the other plankters in the sample under a binocular microscope, and the total numbers of adult females, adult males, immatures and juveniles were counted. If the numbers of M. stellifera were so large that actual counts were impractical, an estimate of total numbers was made by subsampling. In this technique, the sample was first diluted to 500 ml, then shaken vigorously and a 5 ml subsample was removed with a Hensen-Stempel pipette. The subsample was emptied into a watch glass, the total number of M. stellifera counted and the entire subsample was returned to the main sample. This procedure was repeated five times, and the mean of the five subsamples was used to estimate the total number of M. stellifera in the sample. No counts or identifications were made for any other species in the sample.

SCUBA Observations.

The behavior of M. stellifera and associated epifauna and infauna were studied in situ by using SCUBA during summer 1969. The usual method was to enter the water at the surf zone and then to swim slowly and randomly to water depths of 3 and 4 m. Whenever a close bottom inspection was desired, a stationary position was assumed, with the body prone and with the face mask plate two to six inches from the bottom. The water column was occasionally examined for the pelagic presence of M. stellifera, and special attention was given to the response of M. stellifera when bottom sand was agitated by hand in calm water, and by breaking waves in the surf zone. In addition, the composition and configuration of the bottom,

the presence of detritus and the occurrence of potential predators were noted on each dive. Study periods were usually of one hour duration during daylight low tides, and calm and moderately strong surf conditions. All observations were recorded in a field notebook after each dive.

Geographical Range.

Non-quantitative collections were made at coastal beaches from the Gulf of Maine to Long Island, New York, to obtain information on the geographical range and habitat preferences of M. stellifera. Collections were made: 1) in the Gulf of Maine from Cape Small, Maine to Cape Ann, Massachusetts; 2) on the south shore of Cape Cod in the Falmouth-Woods Hole region; 3) at Fire Island, Long Island, New York; and 4) along the Connecticut shore of Long Island Sound to Westport, Connecticut. All samples were taken, by wading, from low water levels on the day of sampling to water depths of 1.0 - 1.5 m.

Additional information was obtained from the examination of the cumacean collections from the Biotic Census of Cape Cod Bay conducted by the Systematics-Ecology Program, Marine Biological Laboratory, Woods Hole, Massachusetts. These collections are deposited in the Marine Biological Laboratory's George M. Gray Museum.

Additional Field Studies.

General observations were made during periodic visits to Jenness Beach and neighboring beaches on the effect of storms on the physical characteristics of the beaches, accumulation of algal detritus on the beach, and in shallow water

following storms, and feeding activities of sea ducks. Stomach contents from sea ducks and bottom fishes were examined from material generously made available by other investigators working in the vicinity of the study area.

Non-quantitative bottom samples were taken under a variety of weather conditions from intertidal sands at water depths of 0 - 1.5 m on flooding and ebbing tides, by skimming a one pint jar over the top few cm of sand, with the mouth of the jar directed forward. Since the sole purpose of this activity was to determine whether or not M. stellifera was present or absent at the time of sampling, neither the sediments nor the animals collected in these samples were retained.

3. Laboratory Studies

Reproduction and Development.

Individual pairs in precopula were isolated from collections made at Jenness Beach in summer 1969 and at Popham Beach, Maine in spring 1970 and placed in covered compartmented plexiglass trays. Each compartment was filled with habitat sea water, and small amounts of sand added for food and borrowing. All specimens were held under refrigeration at the approximate ambient habitat temperature. Preliminary studies showed that M. stellifera could be maintained under these conditions in good health by daily aeration of water and weekly changes of sand and water. Each pair was examined daily for health, molting, and the presence of a brood in the female's marsupium. Animals were considered healthy if they were active, and the molting behavior was studied under a dissecting

microscope whenever an animal was found to be undergoing ecdysis. When a female was known to be ovigerous, the male member of the pair was removed from the compartment and the female cared for in the manner described above for the length of her brooding period, defined as the elapsed time from brood deposition to larval release.

If a female died during her brooding period, her embryos were removed from the marsupium by dissection, placed in a covered stentor dish containing habitat water and held at the same temperature as the other broods of the same group. The embryos were cared for by daily water aeration and weekly water change. Their brooding period was considered over when swimming larvae were present in the dish.

The following data were recorded for each pair: 1) elapsed time from isolation to brood deposition; 2) elapsed time from final female molt to brood deposition; 3) number of molts undergone by each sex; and 4) the length of the brooding period.

Female survivors of the brooding period for the spring 1970 group were retained for the purpose of determining if they could produce a second brood. Each survivor was placed in a separate compartment with two males obtained from the habitat at the end of each female's brooding period. These animals were cared for in the same manner described above.

Rearing of manca larvae from the spring 1970 group to the adult stage was attempted by placing the larvae from each brood in small finger bowls containing habitat water and sand,

holding the specimens at a temperature of 8° C, and changing the water and sand every three or four days.

The behavior of precopula pairs was studied under a binocular microscope, with the specimens in small finger bowls containing habitat water and sand. Camera lucida drawings were made, and photographs were taken of preserved precopula pairs.

Swimming and Burrowing Behavior.

Visual observations were made of swimming animals in large finger bowls containing sea water only, and burrowing behavior of animals in large finger bowls containing sea water and sand. Further details of appendage utilization for these activities were studied under a binocular microscope, with the animals in small finger bowls.

Food and Feeding Behavior.

Animals starved for 24 hrs were placed in small finger bowls containing fresh habitat sand and sea water, and their activities studied under a binocular microscope. Special attention was given to the manipulation of sand grains, an animal's reaction to an encounter with microfauna, and to the response to food offerings. The following potential foods from the habitat were offered: nematodes; pieces of freshly dissected amphipods, isopods and cumaceans; pieces of crustacean exoskeletons, hydroid perisarcs and algal detritus.

Gut contents of freshly collected specimens were examined by first removing the intestinal tract in one piece with a pair of watchmaker's forceps. The gut was then opened in a drop of sea water on a glass slide, a cover slip was added and the preparation studied under a compound microscope.

Substratum Preferences.

A series of experiments were designed to determine the role that micro-organisms adhering to the surfaces of sand grains play as food sources, and to test the extent to which these organisms influence the choice of substratum by M. stellifera. The presence of these micro-organisms was first verified by treating habitat sand with the method described by Meadows and Anderson (1968).

The technique consisted of filling a small finger bowl with sea water (30-33 °/oo) and then introducing two equal volumes of sand into the bowl with a large bore pipette. The sand was added carefully so that the two sands did not mix. A clear, sand-free strip, one-and-one-half inches wide spaning the center of the bowl (hereafter referred to as the buffer zone) separated the two sands. Twenty females, previously starved for 24 hrs, were then placed on the buffer zone. The bowl was immediately placed in a light proof box subsequently kept in a dark refrigerator for 48 hrs at 10° C. At the end of the 48 hr dark period, the box was removed from the refrigerator and a separator was placed in the center of the buffer zone immediately after the box cover was removed. The separator was fashioned from polyethylene to exactly fit the contours of the center of the bowl, and to extend one inch above the water surface. The two sands were thus sealed off and animals were restricted to the area occupied by the sand they had selected. The bowl was then placed next to a lighted desk lamp, and animals were removed one-by-one with a pipette after they emerged from the sand and swarmed at the light source. If the

original number was not accounted for in this way, each sand volume was carefully removed by pipette to expose burrowed animals.

Since experiments took place during peak breeding season, only females were used to eliminate the possibility of sexual attraction exerting an overriding effect, had mixed sexes been used. Males were not used because they were observed to assume precopula with their own sex in the laboratory under crowded conditions.

Sand used in these experiments were collected 1 m below low tide at Jenness Beach and later subjected to the following treatments: fresh sand was collected one day prior to an experiment and held under refrigeration; air-dried sand was dried at room temperature for two weeks; acid-cleaned sand was soaked in concentrated sulfuric acid for 24 hrs and then washed with distilled water ten times. Various combinations of these sands were presented ten times each to M. stellifera. Controls, using fresh sand only, were run with each experiment.

Predation.

Selected species of faunal associates were used for predation experiments. The method consisted of placing a predator-suspect into a large finger bowl, containing sand and sea water, with twenty M. stellifera. The bowl was then placed in a refrigerator at 8° C for 24 hrs. At the end of 24 hrs, the number of surviving M. stellifera were counted, and, if their original numbers had decreased, the bottom of the bowl was examined for M. stellifera remains. Predation

was assumed to be occurring if the number of prey decreased, and an attempt was made to actually observe predation if positive results were obtained. The same number of M. stellifera placed in predator-free bowls under identical conditions served as controls for these experiments. All experiments were repeated five times with the following species: Tryphosella sp., Idotea phosphorea, Edotea triloba, Neomysis americana, Crangon septemspinosus, Pagurus longicarpus and a small specimen of Liopsetta putnami. Although flatfish were known to be present at Jenness Beach, none were captured for predation experiments (see results of SCUBA observations). The flatfish, Liopsetta putnami, was collected from Great Bay, N. H.

Salinity Tolerance Experiments.

Experiments were performed to test the tolerance of M. stellifera to salinities of 5, 10, 15 and 20 °/oo. Ten specimens were placed in covered finger bowls containing the experimental salinities, and held at a temperature of 8-9° C. Specimens were examined at the following intervals: hourly for 5 °/oo, every six hours for 10 °/oo, and every twelve hours for 15 and 20 °/oo. A judgement was made at the time of examination about an animal's health. The two criteria used for life were heart beat and/or appendage movement. Each experiment was repeated four times, and the results were expressed as per cent mortality. A control was run with each experiment, using ten animals per small finger bowl filled with habitat sea water (30-33 °/oo). Experiments with salinities of 10 and 15 °/oo were conducted in summer 1969 with M.

stellifera from Jenness Beach; with salinities of 5 and 20 °/oo in summer 1970 with M. stellifera from Popham Beach, Maine.

4. Drawing Techniques

Camera lucida drawings of small appendages, adults and manca larvae were made with Wild M-5 compound and Wild M-50 binocular microscopes. A Bausch and Lomb microprojector was used for drawings of large appendages. Appendages were prepared for drawing by first dissecting each appendage, with a pair of watchmaker's forceps and a scalpel fashioned from "minuten nadelen", and then mounting each on glass microscope slides in polyvinyl alcohol-lignin pink mounting medium. This was prepared as follows: a stock solution was first made by dissolving 15 g of PVA in 1000 cc of distilled water. A clear stock mounting medium was then made by adding 6.6 cc of melted phenol crystals and 6.6 cc of lactic acid to 16.8 cc of the stock solution. Phenol acts as a fungicide and lactic acid is the clearing agent. Addition of a small pinch of lignin pink to the clear stock solution produced the stain mountant. Specimens were placed directly from the preservative into the stain mountant.

Adults were simply placed in a deep well depression slide flooded with 75% glycerine solution.

Best results for whole specimen drawings of manca larvae were obtained by mounting specimens on microscope slides directly in Hoyer's medium and using plane polarized light.

CHAPTER III

RESULTS

1. Redescription of Mancocuma stellifera, Zimmer, 1943 (Figs. 4-8). The terminology below is after Jones (1963, 1969).

Description of the female.

Carapace: about 30 per cent total length; surface smooth. From dorsal view, tapering evenly posterior to anterior; greatest width 80 per cent of length; two shallow grooves continuing posteriorly from either side of eyelobe for about 70 per cent carapace length; anterior margin rounded, with concave siphonal notch. From lateral view, dorsal surface nearly straight, curving slightly downward anteriorly; eyelobe slightly elevated; pseudorostrum blunt, rounded right anter-lateral angle formed where dorsal and frontal margins join; antennal notch concave, slightly excavated.

Pereon: about 30 per cent total length; surface smooth; greatest width equal to length; five somites distinct from above; first narrowest; third and fourth widest and equal. From lateral view, greatest height 75 per cent length; tergites broaden dorsal to ventral, covering coxae of pereopods; infero-lateral angles of tergites 1 - 4 produced, overlapping; tergites 2 - 4 widest; posterior infero-lateral angle produced on tergite 4, covering 50 per cent of tergite 5.

Pleon: about 40 per cent total length; surface smooth; somite 5 longest, about 20 per cent longer than somite 6; somite 6 only slightly produced between uropods; mid-lateral border

tergites 1 - 4 produced posteriorly; sternites 1 - 4 bearing 2 short setae on mid-posterior border.

Antenna 1: peduncle with 3 segments of approximate equal length. Flagellum two-segmented; distal segment bearing 2 aesthetascs distally. Accessory flagellum one-segmented; about 50 per cent length proximal flagellum segment.

Antenna 2: rudimentary; three segmented. Proximal segment about 40 per cent longer than distal segments combined, bearing 3 plumose spines. Segment 2 less than 25 per cent length proximal segment; segment 3 about 50 per cent length proximal segment; segment 3 tapering proximal to distal, ending in 4 strong spines in groups of 2.

Left Mandible: molar process robust; masticating surface flattened, with row of fine setae on anterior and posterior borders; pars incisiva with 4 teeth; lacinia mobilis with 1 large tooth and 2 long spines; spine row with 5 long and 2 short spines; posterior end pointed.

Maxilla 1: endopodite normal, bearing 2 long filaments of nearly equal length.

Maxilla 2: normal, with 2 upper lobes.

Maxilliped 1: six-segmented, ischium lacking; branchial apparatus with 6 branchiae of approximate equal length, and small accessory lobule.

Maxilliped 2: seven-segmented; ischium smallest; dactylus ending in a claw; rudimentary oostegite bearing 13 slender setae.

Maxilliped 3: broad; basis length equal to remaining segments combined; bearing an exopodite and 7 - 10 plumose setae on ventral surface; dorso-anterior border produced, bearing 4 - 6

plumose spines, covering ischium joint dorsally. Carpus and propodus bearing rows of strong setae on ventral surfaces. Dactylus ending in several long spines.

Pereopod 1: longest pleon appendage, propodus and dactylus extending beyond pseudorostrum tip. Basis broad, about 25 per cent longer than remaining segments combined; bearing an exopodite and 15 - 20 plumose setae on ventral border; distal end produced as collar around ischium joint, with distinct notch on dorso-anterior border. Ischium shortest segment. Merus produced anteriorly and diagonally, ending in short spine. Carpus longest, broadest of three remaining segments; produced ventrally, curving anterior to posterior; ventral border bearing row of strong setae. Propodus about 80 per cent length of carpus; flattens against carpus in subchelate manner; inner surface of ventral and anterior margins bearing strong setae of increasing length posterior to anterior, anterior setae projecting over dactylus dorsum. Dactylus 50 per cent length carapace; inner surface of anterior margin bearing row of strong setae twice dactylus length.

Pereopod 2: 60 per cent length pereopod 1; compact. Basis broad, length almost equals remaining segments combined; bearing exopodite and 8 - 10 plumose setae on ventral border. Ischium shortest, lacking setae. Remaining segments of approximate equal length; merus antero-dorsal border bearing 2 spines; carpus and propodus antero-ventral border bearing 3-4 spines; dactylus ending in 6 - 7 strong spines of unequal length.

Pereopods 3 - 5: relatively short, compact; decreasing in length anterior to posterior. Basis always longest and

broadest segment; ventral border bearing 3 - 4 plumose setae; basis 5 lacking exopodite, exopodite 4 rudimentary, exopodite 3 normal; 90 per cent length ventral border basis 5 bearing row of small teeth. Remaining segments (ischium, merus, carpus) bearing 2 - 5 long spines antero-dorsal borders; carpus and propodus bearing 2 - 3 spines antero-ventral borders; dactylus reduced to claw.

Exopodites: maxilliped 3, pereopods 1 - 3 unusually well-formed for the order; peduncles broad, dorsal borders bearing 0 - 5 plumose setae; flagella six to eight-segmented, each segment bearing long plumose setae. Exopodite 4 peduncle 25 per cent longer than one-segmented flagellum; flagellum lacking setae.

Uropods: peduncle twice length of pleon somite 6; inner surface bearing 6 - 7 short spines, terminal spines finely plumose. Endopodite equals peduncle length; distal segment about 40 per cent length proximal segment, ending in 2 short lateral, 1 long terminal spine, finely plumose; proximal segment inner surface bearing 6 - 8 short, finely plumose spines. Exopodite about 90 per cent endopodite length; proximal segment about 20 per cent length distal segment; distal segment, inner surface bearing 2 - 3 short spines, ending in 4 finely plumose spines of unequal length.

Description of male. Differs from female as follows: Carapace: about 25 per cent total length. From dorsal view, width decreasing only slightly anterior to posterior; greatest width 70 per cent length. From lateral view, entire dorsal surface sloping posterior to anterior; pseudorostrum blunt,

sharp right angle formed where dorsal and frontal margins join; lateral margin curves posteriorly for 30 per cent carapace length forming broadly excavated antennal notch.

Pereon: about 25 per cent total length. From dorsal view, greatest width about 50 per cent length. From lateral view, greatest height 40 per cent length.

Pleon: about 50 per cent total length; somites 1 and 2 bearing pleopods; sternites not bearing setae.

Antenna 1: larger and stronger; flagellum three-segmented, proximal segment bearing 2 aesthetascs.

Antenna 2: relatively short for the order. Peduncle three-segmented, about 30 per cent antenna length; distal segment about 10 per cent longer than remaining segments combined, antero-distal border concave, bearing 3 - 4 long setae and 2 broad teeth (not shown in Figure 5) fitting grooves at base of proximal flagellum segment, postero-distal border bearing 5 shorter setae, posterior border bearing dense row of setae. Flagellum twenty two-segmented; about 10 per cent carapace length; with distinct proximal and distal parts; proximal part ten-segmented; about 40 per cent flagellum length; basal segment longest, with free proximal border concave; remaining segments of approximately equal length, width uniformly decreasing proximal to distal, posterior borders bearing 1 short terminal setae and 2 small recurved spines at mid-length. Distal part twelve-segmented, about 60 per cent flagellum length; segments of equal length, width uniformly decreasing proximal to distal; posterior borders segments 1 - 11 bearing 1 short terminal setae and 2 longer serrate setae at mid-length; segment 12 ending in several long setae.

Pereopod 4: bearing normal exopodite; peduncle lacking setae; flagellum five-segmented.

Pleopods: two-segmented peduncle bearing two rami and strong spine midway on inner border; distal segment about 85 per cent peduncle length. Inner ramus about 60 per cent peduncle length, 50 per cent longer than outer ramus; lying behind outer ramus; inner border bearing minute spine. Both rami ending in 2 setose spines, nearly equal in length, about 50 per cent longer than peduncle.

Color: Brown-black; both sexes, all immature size classes except manca larva possessing one to two patterns in all seasons as follows: 1) pigment lacking, bearing chromatophores as described below (Figs. 1B, 1D); 2) pigmented, chromatophore distribution similar (Figs. 1A, 1C). Chromatophores: dense over entire carapace, sparse on pereon dorsum, sparingly on dorsum, sparingly on dorsum of pleon, antennae, uropods, outer pereopod surfaces. Pigment: entire over carapace; dorsum of pereon, pleon somites 1 and 6, uropod peduncles, posterior two-thirds pleon somite 5, proximal three-quarters peduncle male antenna 2. Sparingly on all other appendages, pereon somite lateral surfaces, lateral and ventral surfaces pleon somite lateral surfaces, lateral and ventral surfaces pleon somite 6, pleon somite 5 lateral surface along line running diagonally antero-dorsal to postero-ventral. Lacking on pleon somites 2 - 4. Larger mature individuals frequently with unpigmented triangular patch with rounded apex, running dorsally for one-half carapace height from posterior margin of antennal notch.

Geographic Range: Mancocuma stellifera was found to inhabit sands below low tide levels at the following Gulf of Maine beaches: 1) Maine - Fort Popham (Kennebec River), Popham Beach, Old Orchard Beach, Kennebunk Beach, Ogunquit Beach, Short Sands, Long Sands and Sea Point Beach; 2) New Hampshire - Wallis Sands, Jenness Beach, North Beach and Hampton Beach; 3) Massachusetts - Good Harbor Beach. All of these beaches are composed of clean, well sorted sand, and all except the Fort Popham beach are exposed to the open ocean. The Fort Popham collection was made approximately one-quarter mile from the open ocean, and it is unlikely that this beach is affected by wave action. The salinity of the water at the time of the Fort Popham collection was made was 27.0°/oo. An average of only two or three specimens were found in the ten samples taken at Fort Popham, while an estimated average of fifty to several hundred specimens were collected in each sample at all other beaches.

Mancocuma stellifera was not found at any beaches sampled south of Cape Ann, Massachusetts, nor in the Marine Biological Laboratories' Systematic-Ecology Program Cape Cod Bay cumacean collection. The latter finding should not be interpreted to mean that M. stellifera does not inhabit Cape Cod Bay beaches, since few of the Program's samples were taken in shallow water close to shore, and the cumaceans in the collection came from material retained by a sieve with a mesh size of 1.0 mm^2, precluding capture of most M. stellifera if they were present.

My collecting data and the reports by Bousfield (1962a) and Zimmer (1943) indicate that M. stellifera's distributional range is from the Gulf of St. Lawrence to Cape Ann, Mass. Mancocuma stellifera should therefore be included with the western Atlantic boreal fauna, since its distribution does not extend south of Cape Cod. More collecting will be necessary before any comprehensive account can be given of the species' complete geographical distribution.

Remarks: Mancocuma stellifera is included in the family Bodotriidae. A closely related species, Mancocuma altera, Zimmer (1943), was reported only once, from Beaufort, North Carolina and the Chesapeake Bay. The range limits of M. altera are not known, nor is it known if the ranges of the two species overlap.

2. Physical Factors

a. Granulometry

Results of granulometric analyses of sediment samples from four seasonal subtidal transects at Jenness Beach, and for the sediment samples from the Wallis Sands and Long Sands subtidal transects are shown in Table 1. These data show that sediments at all three M. stellifera habitats had similar grain size distributions. Mean sand grain diameters at 0 m ranged from 0.260 mm - 0.374 mm, decreased with increasing water depth, and ranged from 0.146 mm - 0.169 mm at 7 m. At water depths greater than 0 m, Jenness Beach mean sand grain sizes were slightly smaller than sand from Wallis Sands and Long Sands.

Figure 4. Mancocuma stellifera Zimmer, 1943. A, male, 3.00 mm, lateral view; B, male, dorsal view; C, female, 3.12 mm, lateral view; D, female, dorsal view.

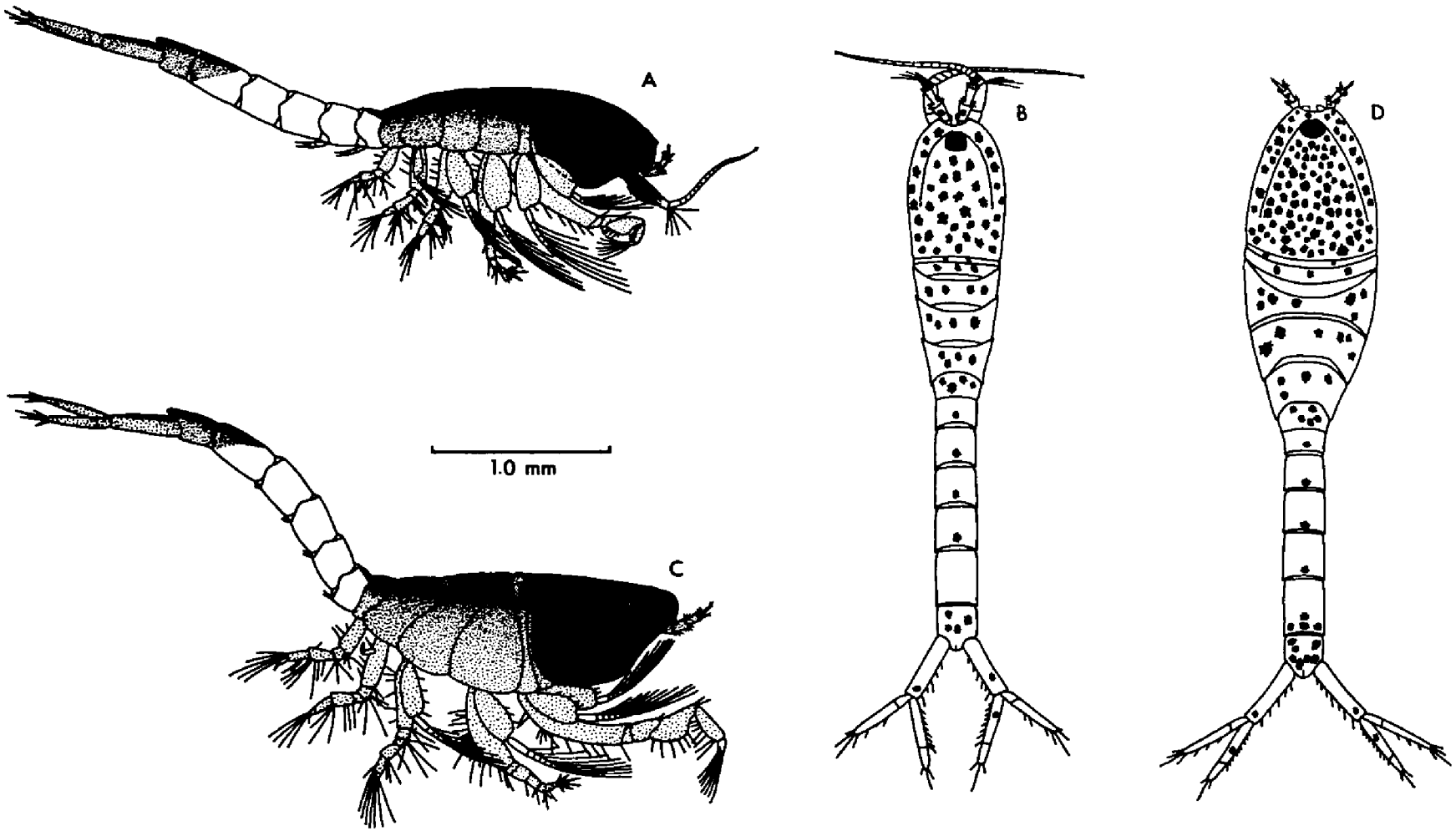
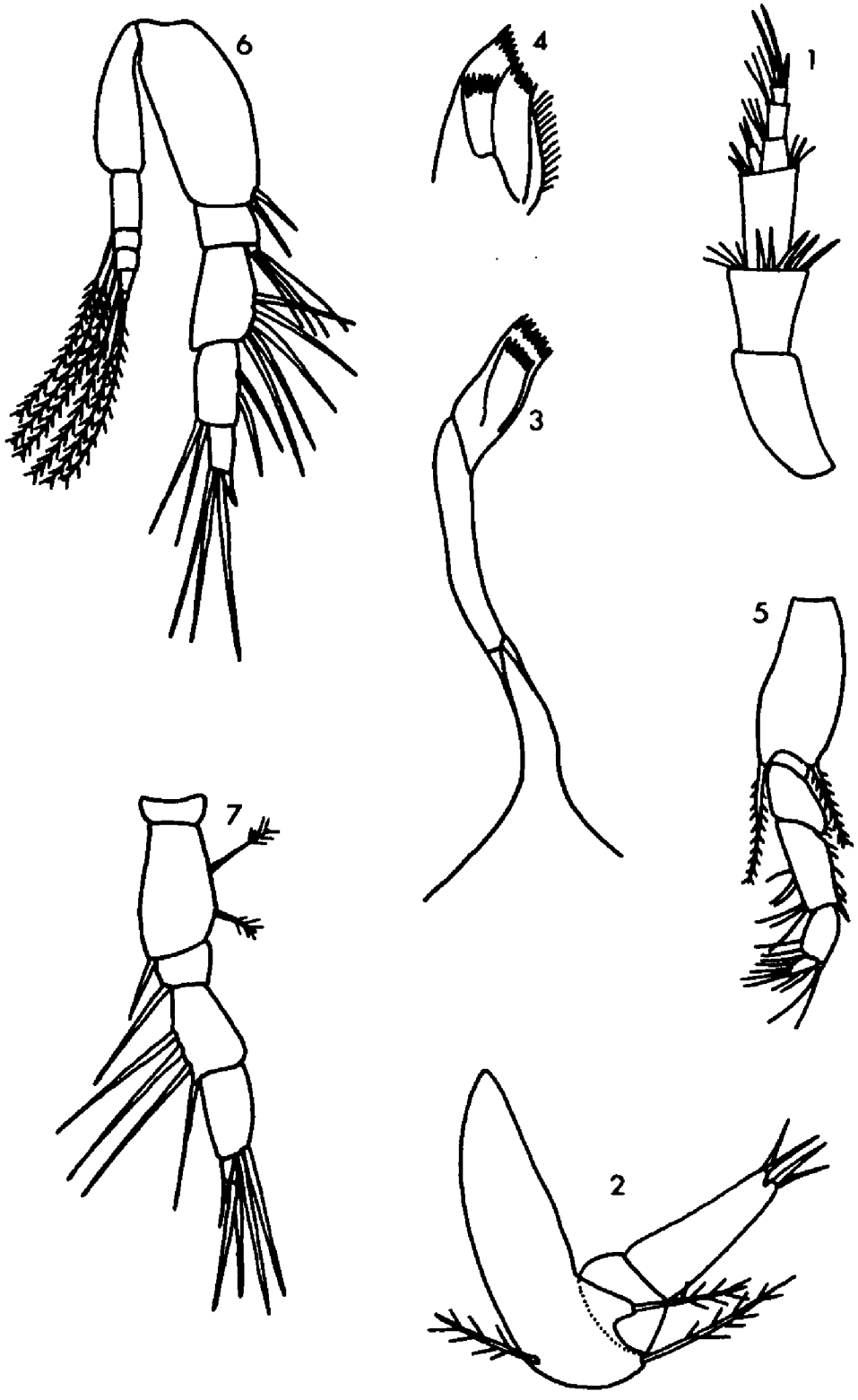

A
B
C
D
1.0 mm

Figure 5. Mancocuma stellifera Zimmer, 1943. Male, 3.00 mm: 1, antenna 1; 5, maxilliped 2; 6, pereopod 4; 7, pereopod 5. Female, 3.12 mm: 2, antenna 2; 3, maxilla 1; 4, maxilla 2.


6
4
1
3
5
7
2

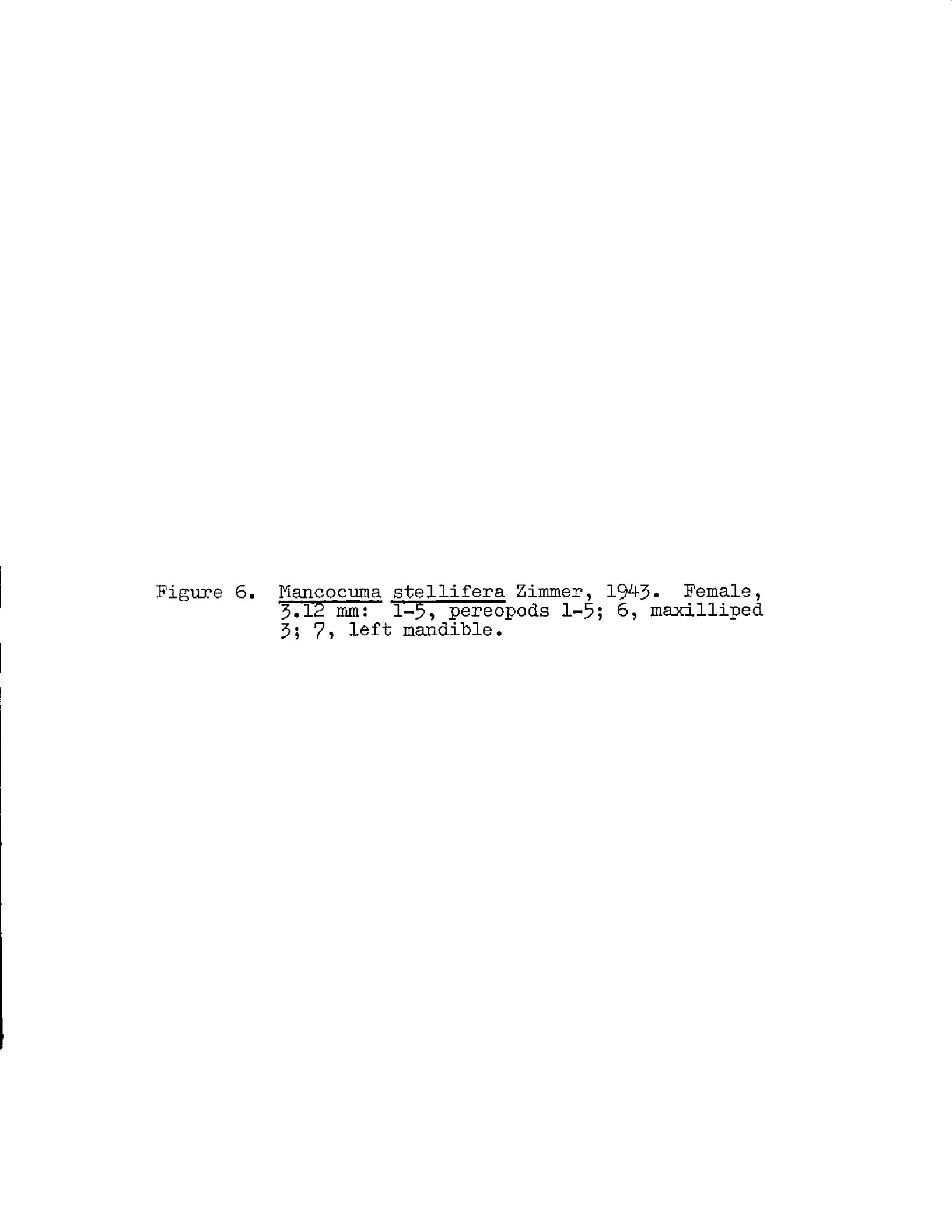


Figure 6. Mancocuma stellifera Zimmer, 1943. Female, 3.12 mm: 1-5, pereopods 1-5; 6, maxilliped 3; 7, left mandible.

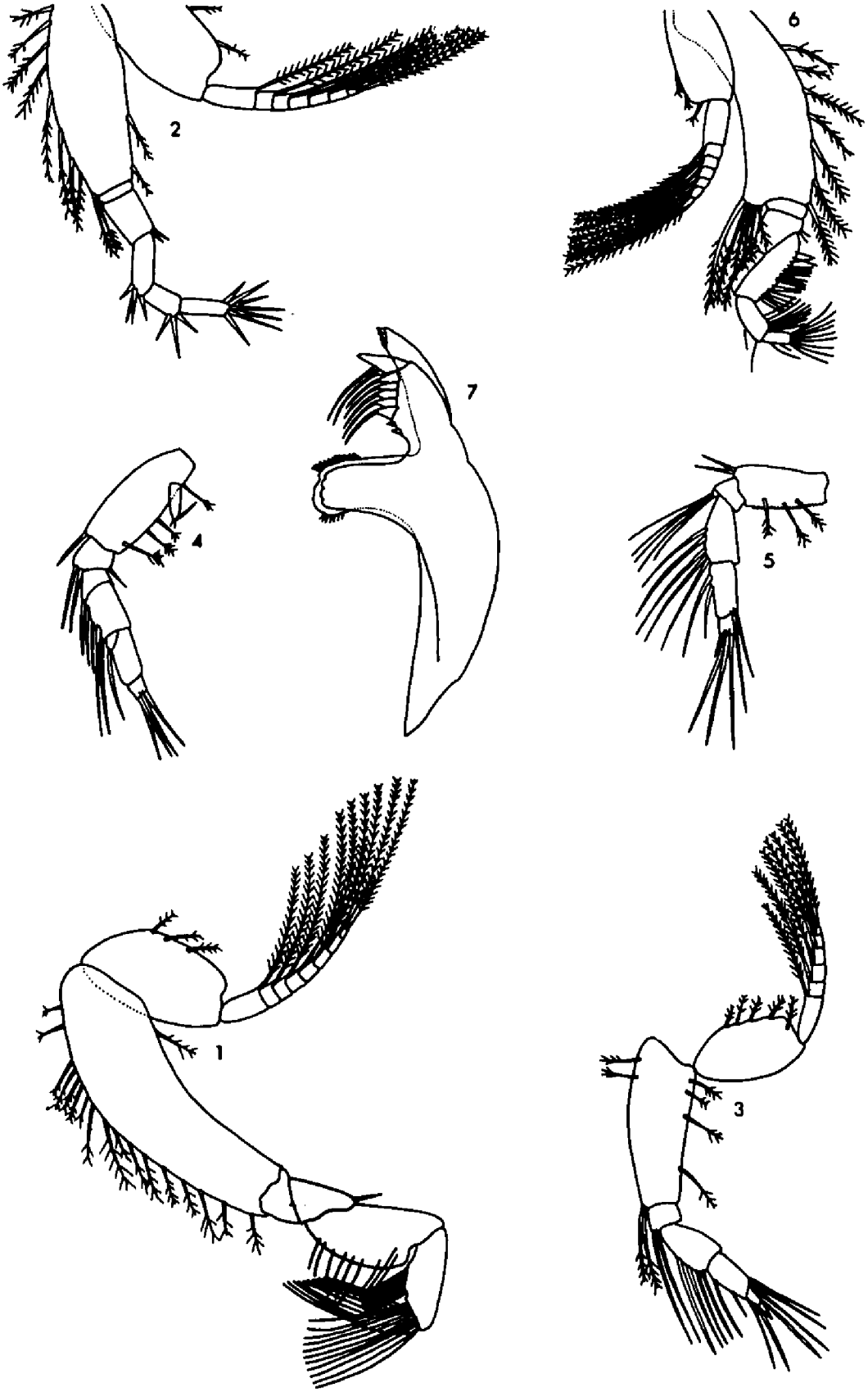
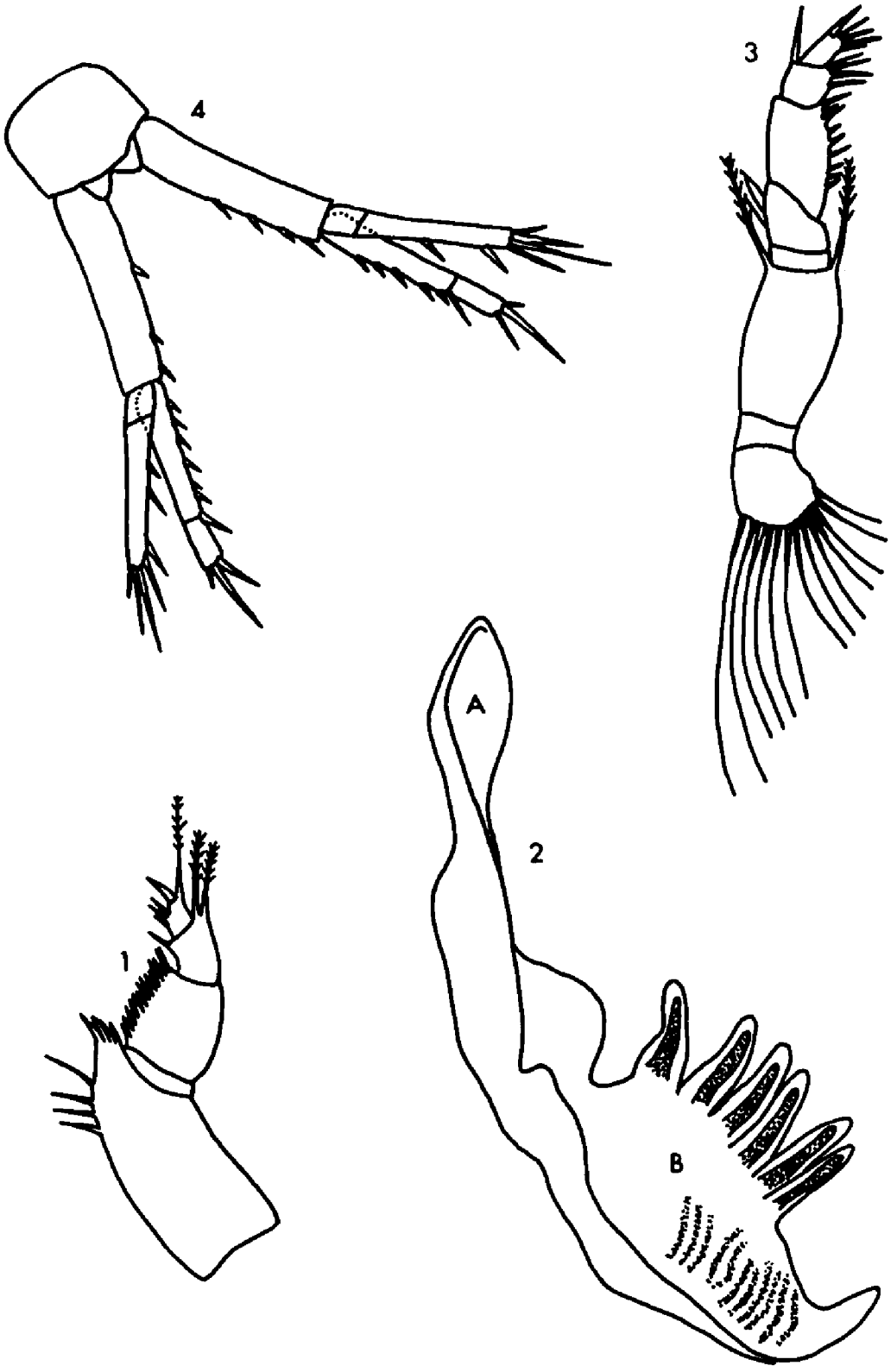

2
6
7
4
5
1
3

Figure 7. Mancocuma stellifera Zimmer, 1943. Female, 3.12 mm: 1, maxilliped 1; 2, maxilliped 1 branchial apparatus, A - siphonal part, B - branchial part; 3, maxilliped 2; 4, pleon somite 6, uropods.


4
3
A
2
1
B

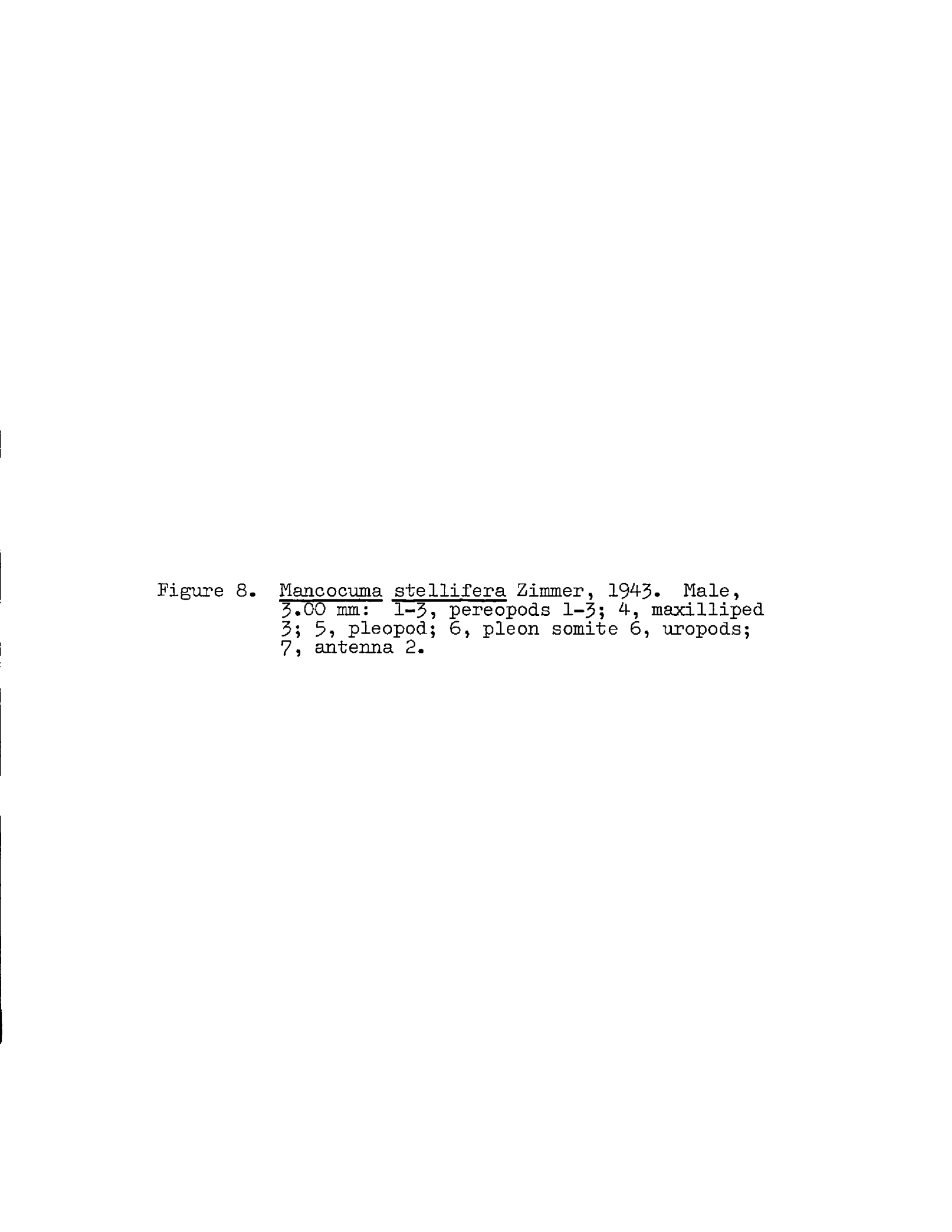


Figure 8. Mancocuma stellifera Zimmer, 1943. Male, 3.00 mm: 1-3, pereopods 1-3; 4, maxilliped 3; 5, pleopod; 6, pleon somite 6, uropods; 7, antenna 2.

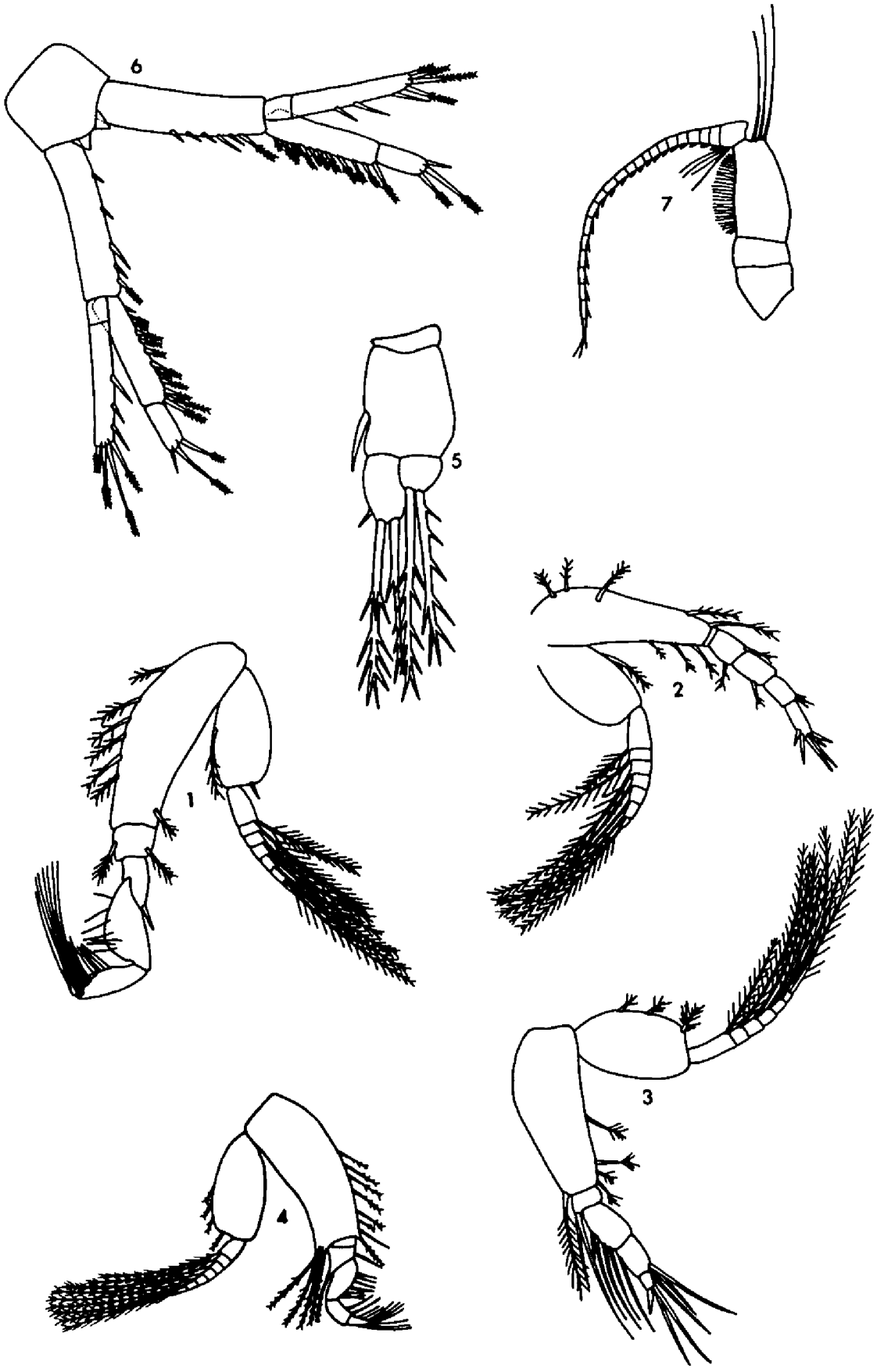

6
7
5
2
1
3
4

Table 1. Mean and grain diameters for subtidal habitats of *M. stellifera*.

Habitat	Jenness Beach			Wallis Sands		Long Sands
	1968 Sept.	1969 Jan.	March	June	July	1970 July
Depth of Water (m)	Mean Diameter (mm)					
0	0.374	0.348		0.370	0.260	0.358
1	0.385	0.250	0.195	0.187		
2	0.243	0.210	0.192	0.188	0.273	0.198
3	0.174	0.187	0.185	0.181		
4	0.174	0.172	0.171	0.171	0.194	0.186
5	0.166	0.174	0.175	0.166		
6	0.156	0.163	0.158	0.152	0.177	0.173
7	0.146			0.147	0.167	0.169

Intertidal transects were run on June 6 and September 3, 1969. Median sand grain diameters of low intertidal sands were considerably larger than subtidal sands (Table 2).

b. Seasonal Temperature and Salinity

Surface water temperature and salinity variation at Jenness Beach for the period July 1968 through December 1969 are shown in Figure 9. Temperatures were highest in late summer and early fall of both years, decreased during fall 1968, were lowest in winter 1969, and increased during spring and summer 1969. Highest and lowest recorded temperatures were 17.7° C in September 1968, and 2.0° C in January and February 1969. Salinities ranged from a high of 34.0°/oo in January 1969, to a low of 28.7°/oo in April 1969. The latter salinity can be attributed to fresh water runoff, from spring snow thaw and rains, into New Hampshire coastal waters in spring 1969.

c. General Observations

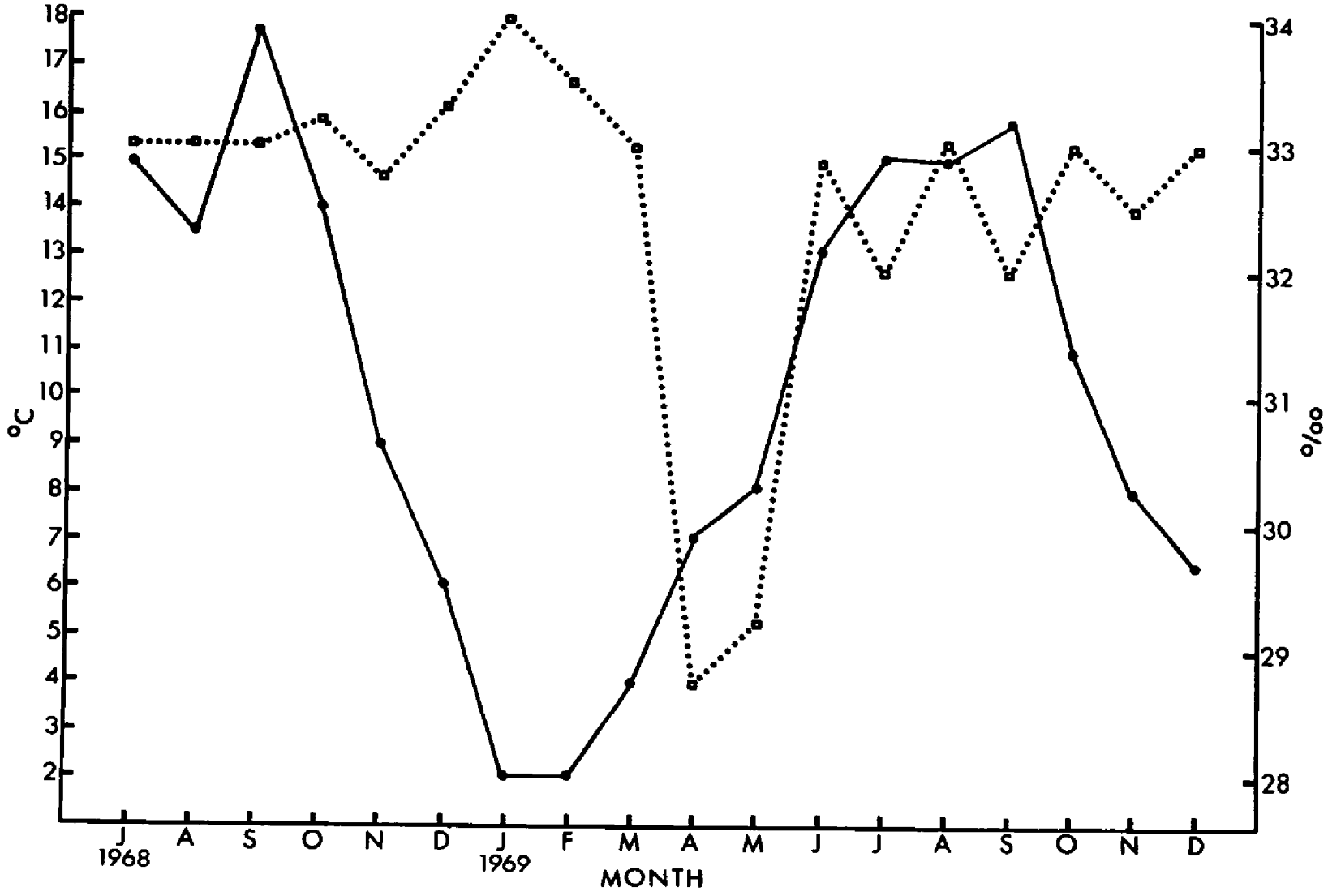
Observations of the physical changes of Jenness Beach during all seasons showed that the beach underwent some of the annual morphological changes that are characteristic of marine beaches (Bascom, 1960). Although no survey was made of the winter intertidal beach profile, it was apparent that heavy winter surf did not appreciably alter the gentle summer intertidal profile (2.69°, summer 1969). A winter berm was established, and the winter berm progressed seaward in summer.

Although no quantitative estimates were made of silt and detritus contents of Jenness Beach subtidal sands, the

Table 2. Mean diameters of intertidal sands, Jenness Beach transect, June 6, 1969.

Horizontal Distance (m)	Mean Diameter (mm)
H.W.	0.373
30	0.544
60	0.512
90	1.369
120	1.215
L.W.	0.369

Figure 9. Seasonal surface temperatures (solid line) and salinities (dotted line) for Jenness Beach, July 1968 - December 1969.


°C
‰
MONTH
J
1968
A
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1969
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D

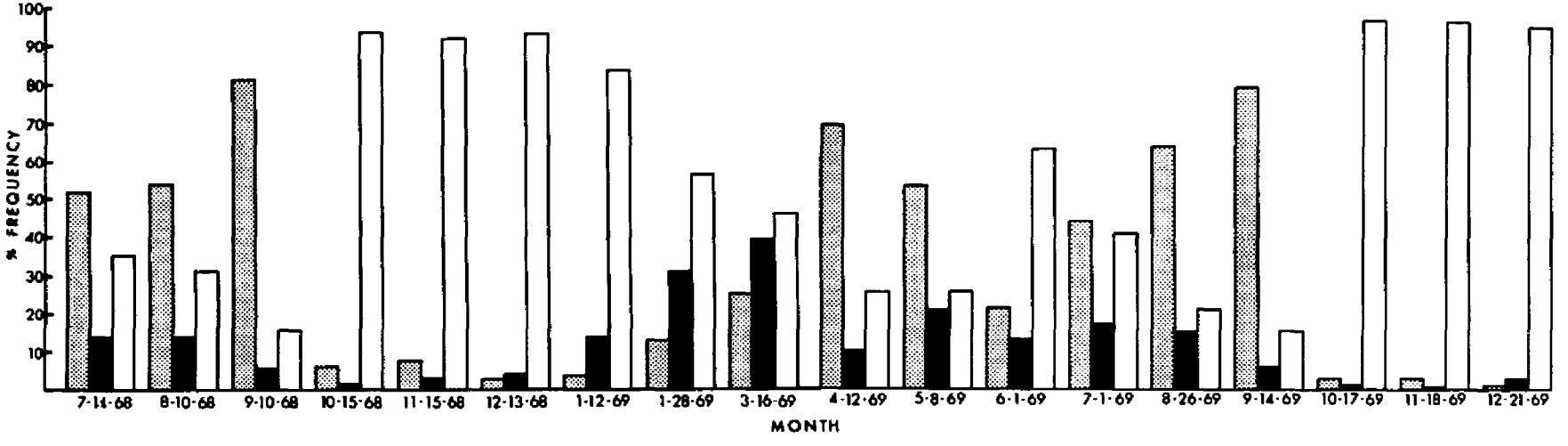
following generalizations are presented on seasonal observations, in situ underwater observations, and examinations of transect dredge samples. Sands from water depths of 0 - 3 m below low water levels appeared to contain little silt, but silt increased in sands from water depths of 4 - 7 m. Large particulate algal detritus was consistently found in and on sands at water depths of 0 - 3 m, but it occurred with decreasing frequency as the depth of overlying water increased. This detritus originated from degraded algae in storm deposited beach wrack, and it was most abundant after winter and spring storms.

Accumulations of animal detritus, composed largely of crustacean exuvia, appeared to be most abundant in shallow water subtidal sands during summer months.

3. Population Biology

a. Sexual Biology. Data for reproductive cycles (Fig. 10) show precent frequencies for ovigerous females, mature males and immatures (maturing and juvenile animals) for 57,839 M. stellifera collected in Jenness Beach population samples from July, 1968 to December, 1969. Reproduction was continuous, but at lowest intensities during fall and winter of both years. The data show two consecutive reproductive cycles: 1) from October, 1968 to June, 1969; 2) from June to October, 1969. Reproductive peaks, represented by maximum percentages of ovigerous females, occurred in September, 1968 (81.2%), April, 1969 (69.4%), and September, 1969 (78.6%). New generations entering the population in months following reproductive

Figure 10. Reproductive cycles of M. stellifera at Jenness Beach, July 1968 - December, 1969. Stippled areas, ovigerous females, solid areas, mature males; clear areas, immatures.


% FREQUENCY
100
90
80
70
60
50
40
30
20
10
7-14-68
8-10-68
9-10-68
10-15-68
11-15-68
12-13-68
1-12-69
1-28-69
3-16-69
4-12-69
5-8-69
6-1-69
7-1-69
8-26-69
9-14-69
10-17-69
11-18-69
12-21-69
MONTH

peaks are represented by maximum percentages of immatures in October, 1968 (93.2%), June, 1969 (63.6%) and October, 1969 (96.7%). The slight increase of immatures from 91.4% in November to 93.6% in December, 1968 is discussed below in relation to population changes (Fig. 11).

Male per cent frequencies decreased to low value during fall and early winter months, indicating probable occurrence of male mortalities at these times.

Female population changes are discussed below (Fig. 11), since data in Figure 10 do not distinguish sexually immature from interbrooding females, that were collectively defined as immatures for reproductive cycle data.

Fecundities of 729 female M. stellifera examined in 1968 and 1969 are shown in Table 3. Fecundities peaked in October and December, 1968, and in June and September, 1969. Fecundity remained essentially the same during summer 1968 and 1969, decreased during winter 1968-1969 and fall 1969, but increased during spring 1969. Table 4 shows that larger females carried larger broods during 1969, and that female of any given body length generally carried larger broods during May, June and September, 1969. Mean monthly brood sizes for 1969 ranged from 2.0 to 23.3 (Table 4). The embryos of any given brood were found to be in the same stage of development.

Table 5 gives sex ratios for mature male and ovigerous female M. stellifera collected in population samples in 1968 and 1969. Ovigerous females were dominant for all months except December, 1968, 1969 and January through March 1969.

Figure 11. Length frequency histograms of M. stellifera from Jenness Beach, January - December, 1969. Females above the line; males below the line. Shaded areas, ovigerous females; solid areas, mature males; clear areas, maturing females and males.

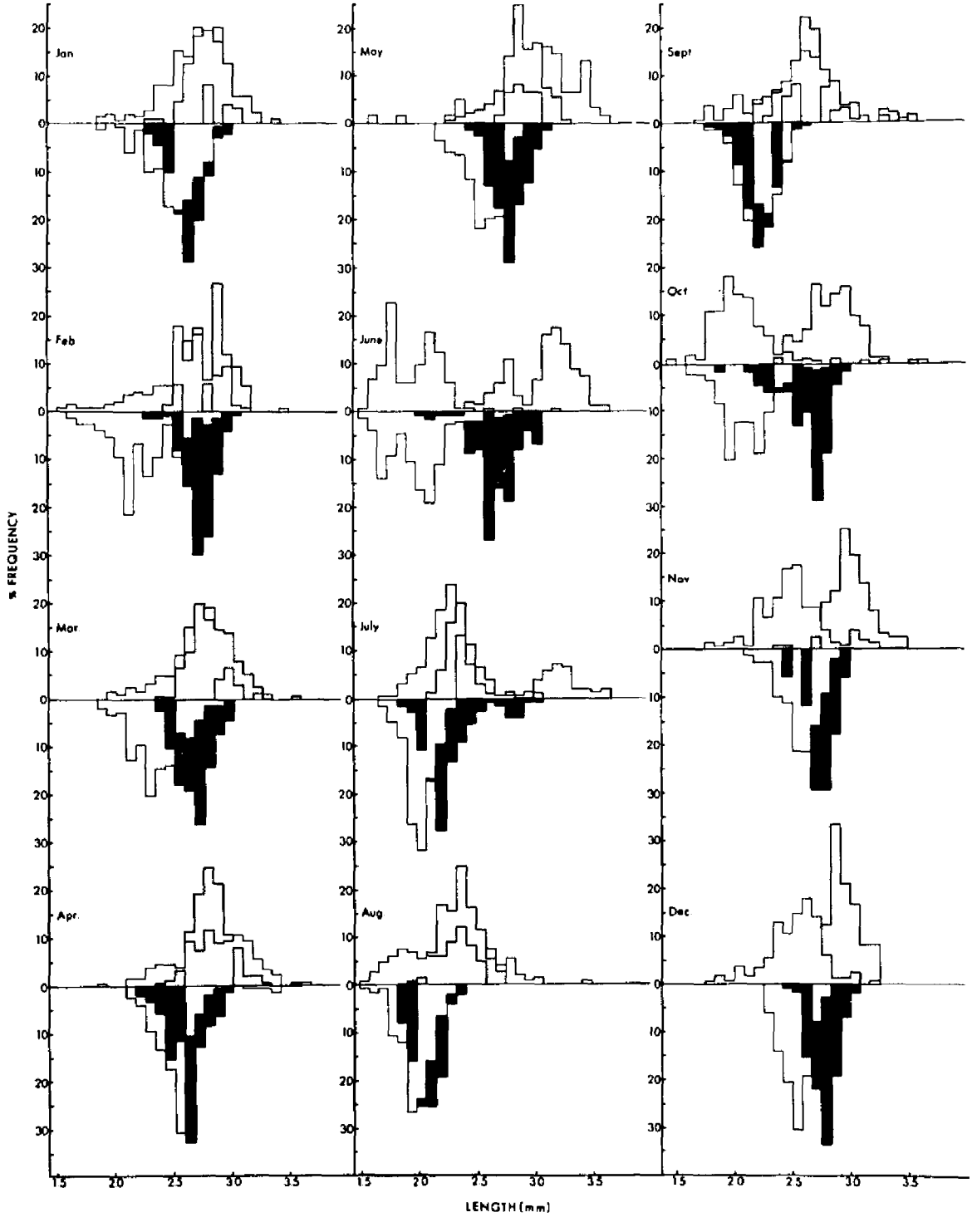

Jan
Feb
Mar
Apr
May
June
July
Aug
Sept
Oct
Nov
Dec
% FREQUENCY
LENGTH (mm)
15
20
25
30
35

Table 3. Fecundity of M. stellifera at Jenness Beach, July 1968 - December 1969.

Date	Number of Females	Fecundity
7-14-68	50	5.36±3.03*
8-10-68	49	5.49±2.35
9-10-68	50	6.52±2.07
10- 1-68	50	8.04±2.40
11-16-68	17	6.05±2.56
12-13-68	39	8.23±2.20
1-28-69	11	4.27±1.23
3-10-69	50	5.84±1.57
4-12-69	50	6.43±2.24
5- 5-69	47	9.21±4.22
6- 1-69	50	11.62±4.79
7- 1-69	50	7.50±4.59
7-29-69	50	7.23±2.70
9-14-69	50	10.74±4.44
10-17-69	49	9.63±3.31
11-16-69	47	7.51±2.29
12-21-69	20	5.45±0.99

* ± 1 standard deviation

Table 4. Mean brood sizes of *M. stellifera* at Jenness Beach, 1969.

Female Size Class (mm)	Mean Brood Size										
	Jan	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
2.16-2.24						4.0	4.0				
2.28-2.36						4.3		5.0			
2.40-2.48		7.0			4.0	3.9	5.5	6.0	6.0		
2.52-2.60	2.0			11.0		4.5	5.3	8.0	6.0		
2.64-2.72	4.0	5.0		6.5	6.0	4.0	5.2	9.2	7.9		
2.76-2.84	4.3	5.8	6.2	6.7	6.0	4.0	9.0	10.5	10.5	6.1	5.2
2.88-2.96	5.0	5.3	6.0	7.4			9.7	11.9	10.3	6.0	5.3
3.00-3.08	4.7	6.6	6.6	11.2	10.5	13.7	11.3	13.2	10.0	7.9	5.7
3.12-3.20	5.0	5.9	6.6	13.7	11.9	10.5	7.8		13.8	9.3	6.0
3.24-3.36		8.0	8.5	23.0	13.1	12.3	9.3	15.4	9.0	9.0	
3.40-3.48					13.8	11.8	11.3			9.0	
3.52-3.60		8.0	6.0		19.0	11.0		16.0			

Table 5. Sex ratios of M. stellifera from Jenness Beach, 1968 - 1969.

Date	Sex Ratio (Male:Female)
1968	
7-14	1 : 3.61 (1678)[1]
8-10	1 : 3.77 (649)
9-10	1 : 17.56 (297)
10-15	1 : 6.40 (296)
11-15	1 : 3.25 (17)
12-13	1 : 0.83 (163)
1969	
1-11	1 : 0.23 (318)
1-28	1 : 0.40 (250)
3-16	1 : 0.87 (560)
4-12	1 : 6.66 (2582)
5-8	1 : 2.50 (2772)
6-1	1 : 1.71 (1430)
7-1	1 : 2.85 (2224)
8-26	1 : 4.25 (4756)
9-14	1 : 13.40 (5084)
10-17	1 : 3.66 (303)
11-18	1 : 20.33 (128)
12-21	1 : 0.19 (145)

1 - Number of animals

Females were most dominant in September 1968, 1969, and November 1969. However, the latter sex ratio was based on a total of only 17 individuals. Male:female ratios approximating 1:1 occurred only during spring and summer breeding periods, March and June 1969, respectively. Sex ratio peaks favoring females correspond with peaks of ovigerous females present in April 1969 and September 1968, 1969 (Fig. 10).

The annual changes in the composition of the M. stellifera population at Jenness Beach for 1969 are shown in Figure 11. These data represent per cent length frequencies for subsamples of 17 - 150 animals of four of the five life history stages defined earlier, i.e., mature males, mature (ovigerous) females, maturing males and maturing females. Juveniles were not measured, and a distinction was not made between the degrees of sexual maturity of maturing female size classes. However, for a given month, maturing females, i.e., possessing secondary sex characteristics but lacking fully developed oostegites, as large as, or larger than the smallest ovigerous females, had previously produced broods and were in interbrooding periods; while maturing females smaller than the smallest ovigerous females were sexually immature.

The February, June and October histograms (Fig. 11) show recruitment to the population. These are defined as winter, spring and summer generations, respectively, constituting the length-frequency modes on the left of the histograms. Survivors of previous generations constitute the length-frequency modes on the right of the histograms. The February-

April, June-August and October-December histograms show the growth and maturation of these generations. Length-frequency modes of new generations shift from left to right, as these generations eventually replace older generations, whose length-frequency modes concurrently shift from left to right.

The 1969 winter generation was produced by older 1968 summer females, or younger 1968 fall females. The January-April histograms show the winter generation maturing during late February and March. These winter animals joined overwintering 1968 animals to form the 1969 spring breeding population in March. The largest females (body length 3.40-3.68 mm) in the January-April histograms represent overwintering 1968 summer females. The spring breeding population produced the summer generation in late May - early June. The gradual disappearance of spring breeding males is clearly shown in the May-August histograms. Largest males in July (body length 2.72-3.00 mm) represent surviving spring-breeding males. By August, these males were entirely lacking.

The trimodal distribution of maturing and ovigerous females (body length 2.32-3.60 mm) in May is interpreted as follows. All of the females with body lengths 2.32-3.28 mm participated in spring breeding. The larger of the two maturing female size classes (body length 3.20-3.60 mm) were older 1968 females that produced more than one brood; the smaller size class (body length 2.72-3.16 mm) were younger 1968 females and 1969 winter females that produced late spring broods. All maturing females mated in late May, and they appear as the larger ovigerous females in the modes on the

extreme right of the June and July histograms (body length 3.00-3.60 mm). These females contributed to summer recruitment, as did females from the spring breeding population, that continued to reproduce following the release of the 1969 summer generation in late May. The smallest ovigerous females with body lengths 2.48-2.96 mm in the June histogram, and the smaller ovigerous females with body lengths 2.80-3.28 mm in the right mode of the July histogram represent these latter females. The largest females (body length 3.24-3.80 mm) in August through October histograms represent the remnants of the 1969 winter generation.

The 1969 summer generation matured rapidly during June and early July. By August, it had virtually replaced all previous generations. These 1969 summer animals commenced breeding in late June, and they continued to breed throughout the summer and into late fall. This activity provided the entire fall generation in October and the major segment of recruitment from July to December.

Data for reproductive cycles (Fig. 10) show that males decreased in the population from August to November 1968, and from March to April 1969. By correlating these data with the October-December, January-April and March-May histograms (Fig. 11), it is apparent that older males were gradually replaced by maturing males of succeeding generations during these months.

No definite judgements can be made about the times when significant female mortalities occurred, since reproductive cycle data (Fig. 10) do not accurately reflect precent

frequencies for the different maturing female size classes, and data for population changes (Fig. 11) were derived by subsampling. However, female longevity can be inferred from Figure 11. The histograms show that females from each generation followed slower growth and maturation trends than males. Beginning with the summer generation, females continued to grow and reproduce through December 1969. Assuming that 1968 and 1969 population changes were similar, then the largest females in the January-April histograms represent 1968 females. Likewise, 1969 fall female longevity is inferred by the October-December and January-July histograms. Growth, maturation and replacement of 1969 winter females are clearly shown in the February-October histograms.

The annual reproductive cycle of M. stellifera is summarized as follows. Two distinct generations were produced annually, one in early fall, the other in early summer. Reproduction was however, continuous throughout the year, but at lowest intensities during winter. Some fall individuals matured rapidly, reproduced in late fall and provided part of winter recruitment. The major segment of the fall generation over wintered as immatures, then matured in early spring and formed the bulk of the spring breeding population. In the spring, overwintering fall males matured earlier than overwintering fall females. Winter recruited individuals followed the same pattern and joined the spring breeding population. Mortality of spring breeding fall males was high following spring breeding; some fall males survived until mid-summer. Spring breeding females continued to reproduce after juveniles

of the summer generation left their marsupia in May - June. Of these females, all females from the previous fall generation died by the end of summer, but some winter recruited females lived until October. The summer generation matured more rapidly (smallest body lengths: male, 1.80 mm; female, 2.00 mm) than fall and winter individuals. The summer generation provided continuous summer recruitment and gave rise to the entire fall generation. Male mortality was again high in late summer - early fall; surviving summer males lived until mid-winter. Summer females either continued to reproduce throughout fall and winter, after releasing the fall generation in October, or they overwintered as immatures. Surviving summer females joined the following spring breeding population. Oldest summer females lived until the following May.

Estimated life spans differed significantly for sexes. Males reached maximum body length of 3.40 mm and lived for 6 to 7 months, whereas females reached maximum body length of 3.68 mm and lived for 10 to 11 months.

b. Abundance and Density. Data for mean densities and subtidal zonation of M. stellifera at three habitats are shown in Table 6. Jenness Beach data represent 56 duplicate samples taken during eight months, since either adverse weather and sea conditions, or equipment malfunction precluded transects during November and December 1968, and February and April 1969. Also, a boulder pavement and heavy surf precluded Jenness Beach collections at 5 m in September 1968 and 0 m in March 1969, respectively. Six duplicate samples were taken

Table 6. Density estimates for habitats of *M. stellifera*. JB, Jenness Beach; WS, Wallis Sands; LS, Long Sands.

Habitat	JB	JB	JB	JB	JB	JB	JB	WS	JB	LS
Date	9-16 1968	10-15	1-12 1969	3-16	5-19	6-17	7-16	7-2	8-30	6-24 1970
Low Water Height (m)	+0.70	+0.70	0.0	-0.27	-0.30	0.0	0.0	-0.51	-0.51	-0.30
Depth of Water (m)	Mean Density/0.023 m^2									
0	30.0*	293.5	0.0	NS	0.0	0.0	0.0	5.5	52.5	98.5
1	55.0*	902.0	113.5	204.0	153.0	135.0	334.0	365.5	916.5	486.0*
2	44.5	767.0	647.5	97.0	126.0	159.5	85.0	25.0	133.5	889.5
3	170.5	283.0	237.5	197.0	31.5	105.5	43.0	147.5	16.0	395.0*
4	67.5	23.0	67.0	5.0	32.0	125.5	21.0	69.5	68.0	322.5
5	NS	2.0	5.0	3.0	5.5	21.0	68.0	15.0*	23.0	127.0*
6	4.0*	4.0	6.0	2.5	3.0	21.5	78.0	5.0*	22.0	13.0
7	1.0*	0.0	0.0	0.0	7.0	0.0	34.0	3.5	33.5	29.0
Habitat Mean Density	94.2	312.1	179.4	84.8	69.6	94.7	94.8	96.4	158.1	270.5
Standard Error	±32.4	±53.2	±8.1	±8.0	±6.2	±6.9	±17.8	±5.4	±42.7	±33.9
Coefficient of Variation[1]	34.4	17.1	4.5	9.5	8.9	7.3	18.7	5.6	26.9	12.6
95% Confidence Limits	±64.8	±106.4	±16.2	±16.0	±12.4	±13.8	±35.6	±10.8	±85.4	±67.8

1 - S.E./Mean x 100
* - Only one sample taken
NS - No sample

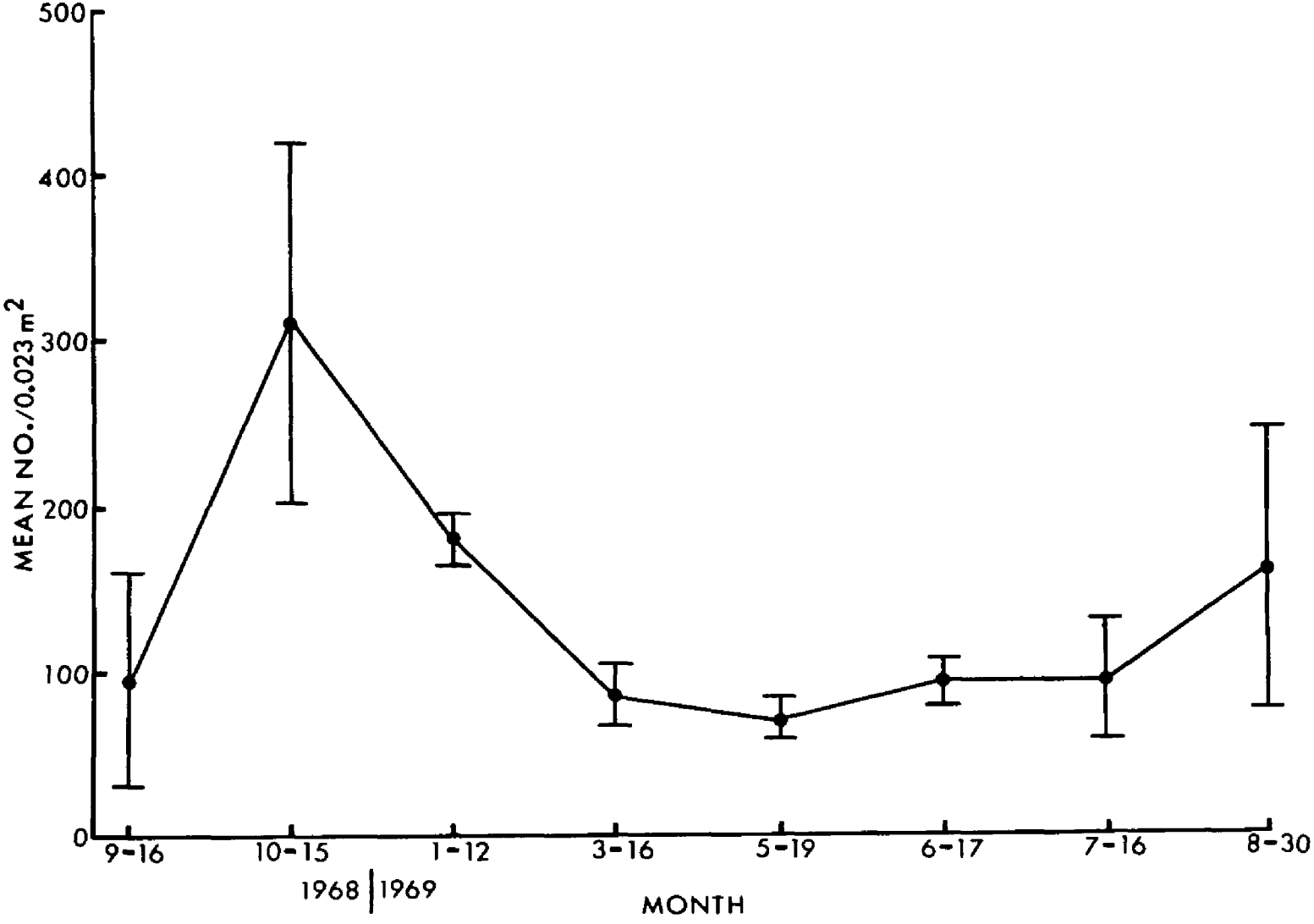
at Wallis Sands and five duplicate samples were taken at Long Sands.

Mean habitat densities and 95% confidence limits for the Jenness Beach population (Fig. 12) show that density was greatest in October 1968, decreased over winter and spring, fell to its lowest in early summer and then steadily increased throughout mid and late summer 1969. Ninety-five per cent confidence limits show that significant density changes occurred in September and October 1968, and in January and March 1969. The more than two-fold density increase from September to October 1968 correlates with data on population reproductive cycles and population changes as discussed earlier. Similar changes occurred from September to October 1969.

Coefficients of variation for mean densities for Jenness Beach (Table 6) fall below 17.1% for all months except September 1968, and July and August 1969. Since the September 1968 coefficient of variation was the highest for all months, it should be noted that this was the first transect made, and was presumably subject to greater collecting errors. In addition, the mean density estimate for September 1968 is based on duplicate samples from water depths of 2 - 4 m only.

The mean density estimate for the July 1969 Wallis Sands transect is nearly equal to the mid-summer 1969 density estimates for Jenness Beach, whereas the second highest of all M. stellifera density estimates, 270.5/0.023 m^2, was obtained for the Long Sands transect in June 1970 (Table 6). The Long Sands value was three times greater than the mean density estimate for Jenness Beach in June 1969.

Figure 12. Habitat mean density estimates of M. stellifera for eight subtidal transects at Jenness Beach. Vertical lines indicate 95% confidence limits for density estimates.


500
400
300
200
100
0
MEAN NO./0.023 m2
9-16
10-15
1-12
3-16
5-19
6-17
7-16
8-30
1968
1969
MONTH

c. Subtidal Zonation. Density estimates (Table 6) and subtidal zonation diagrams (Fig. 13) show that over 90% of the M. stellifera population at Jenness Beach occurred at water depths of 0 - 6 m in June and July 1969, and from 0 - 4 m on all other transects. Highest densities were at 3 m in September 1968, and at 1 or 2 m for all other months. The only differences in zonation of sexes occurred in June, July and August 1969, when 87.8 - 100.0% of M. stellifera collected at water depths of 5 - 7 m were small juveniles (body length 0.8 - 1.4 mm) and manca larvae (Table 7).

Nearly identical results were obtained for the Wallis Sands and Long Sands transects (Tables 6 and 7; Fig. 14). At Wallis Sands, the population density was greatest at 1 m, 96.3% of the population occurred at water depths of 0 - 4 m, and 87.7 - 100.0% of M. stellifera from water depths of 5 - 7 m were small juveniles and manca larvae. At Long Sands, 98.2% of the population occurred at water depths of 0 - 5 m, density was highest at 2 m, and small juveniles and manca larvae comprised 73.3 - 94.8% of the population at water depths of 5 - 7 m.

There was a correlation between the subtidal distribution of M. stellifera and low water tidal heights at all habitats. By using MLW in Figures 13 and 14, and low water heights in Table 6 as reference points, a shift in population distribution is evident. This was seaward and shoreward on spring and neap tides, respectively, hence keeping the main segment of the populations within the 0 - 4 m water depth ranges.

Figure 13. Subtidal zonation of M. stellifera for five seasonal subtidal transects at Jenness Beach.

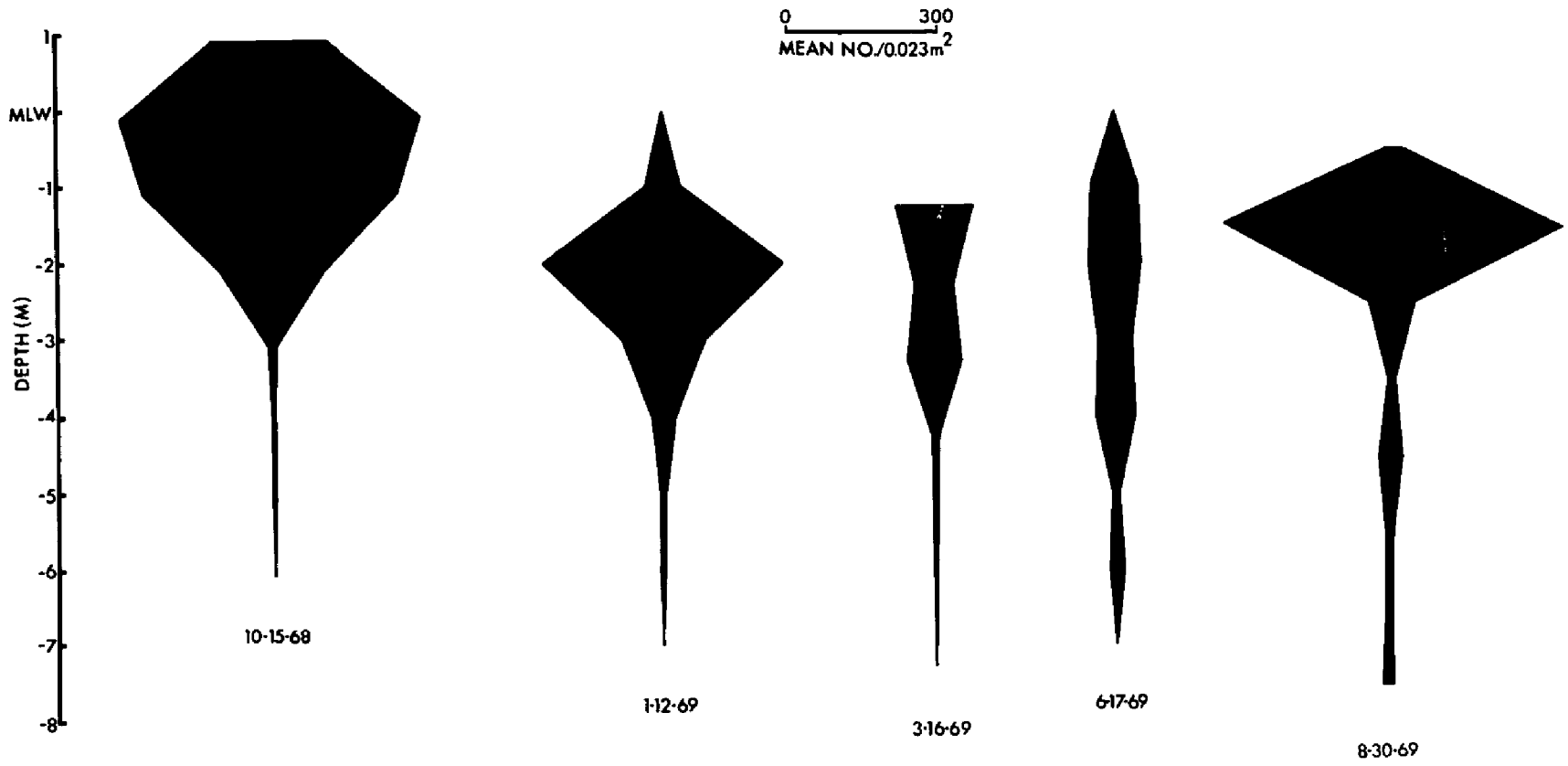
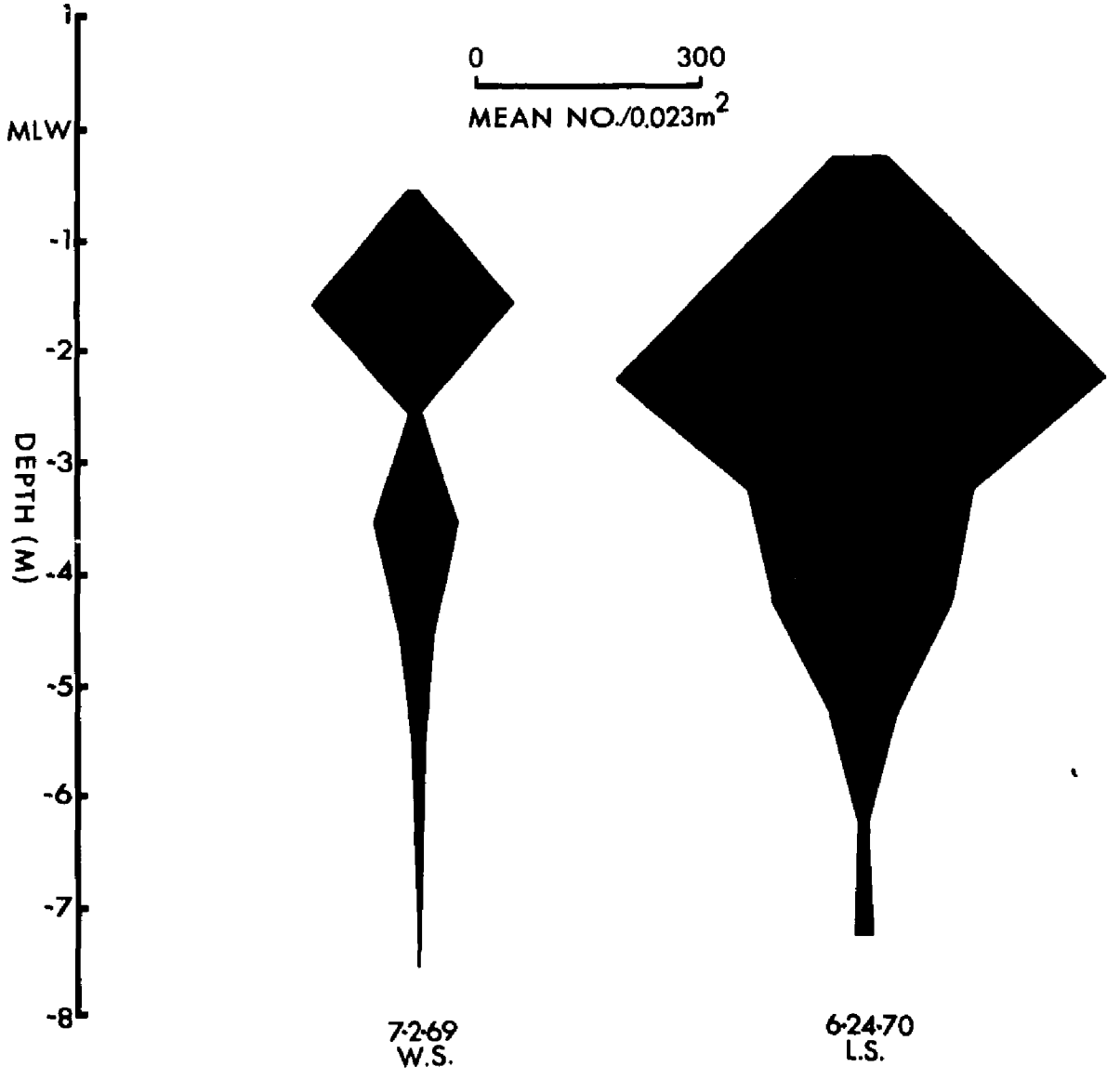

0
300
MEAN NO./0.023m²
DEPTH (M)
1
MLW
-1
-2
-3
-4
-5
-6
-7
-8
10-15-68
1-12-69
3-16-69
6-17-69
8-30-69

Table 7. Juvenile (0.8-1.4 mm) and manca larvae as per cent of total M. stellifera population for four subtidal transects.

Depth (m)	Jenness Beach June	July	August	Wallis Sands	Long Sands
5	87.7	80.8	93.4	100.0	93.7
6	100.0	96.1	95.5	100.0	73.3
7	100.0	95.5	100.0	85.7	94.8

Figure 14. Subtidal zonation of *M. stellifera*. W. S., Wallis Sands; L. S., Long Sands.


1
MLW
-1
-2
-3
-4
-5
-6
-7
-8
DEPTH (M)
0
300
MEAN NO./0.023m^2
7-2-69
W.S.
6-24-70
L.S.

Data for two high water transects taken at Jenness Beach in 1969 at times of high water are shown in Table 8. Mancocuma stellifera was not collected at water depths of 0, 1, and 2 m on June 10, 1969, and at 0 and 1 m on September 6, 1969. Highest densities of M. stellifera were at 4 m on June 10 and at 3 m on September 6. Considering the mean tide range at Jenness Beach, 8.7 ft (2.6 m), and the high water heights on the day of each transect, the water depth over the beach at the time of each transect that corresponded to succeeding mean low water levels (0.0) on these dates were 2.65 m on June 10, and 2.32 m on September 6. Table 8 shows that M. stellifera was not collected at water depths of less than 3 m on June 10 and 2 m on September 6, indicating little movement of the population onto the intertidal beach habitat when it was flooded.

Non-quantitative samples were taken periodically in summer, autumn and spring 1968 - 1970 in New Hampshire, at Jenness Beach, Wallis Sands and Hampton Beach, and in Maine, at Ogunquit Beach, Long Sands and Short Sands (York Beach) and Popham Beach. Mancocuma stellifera was not collected in samples taken from intertidal sands higher than mid-intertidal levels, at times of flooding and ebbing tides, or in samples taken at water depths of 0 - 1.5 m below high water levels. When M. stellifera was collected from intertidal sands, its numbers were few. The species was collected in abundance at all habitats from water depths of 0 - 1.5 m below low water levels, in calm, moderate and strong surf conditions. When M. stellifera was collected at mean low water levels (0.0 m)

Table 8. Density estimates of *M. stellifera* for Jenness Beach high water transects.

Date of Transect	6-10-69	9-6-69
H. W. Height (m)	2.65	2.32
Depth of Water Over Beach (m)	Mean Number per 0.023 m^2	
0	0.0	0.0
1	0.0	0.0
2	0.0	28.5
3	21.5	130.0
4	213.0	96.0
5	97.5	129.0

it was most abundant on spring tides during spring and summer months.

4. Faunal Associates

Thirty-two species representing five phyla constituted the macrofaunal associates of M. stellifera at Jenness Beach for four seasonal subtidal transects, taken in October, 1968 and January, March and August, 1969. The species, their taxa, abundances, mean densities and horizontal distributions along these transects are shown in Tables 9 - 12. The range of individual species' mean densities for all months was 0.5 - 1183.0 animals per 0.023 m^2. The highest and lowest total mean densities occurred in January and March, 1969, respectively, primarily dependent on density variations of the amphipod species.

Table 13 summarizes mean densities of all species, including M. stellifera, at all depths along the transects. All but eleven of the thirty-two associated species were collected on all transects, and, of those species consistently present, Bathyporeia quoddyensis had the highest densities for every month. In addition, B. quoddyensis was the only species that occurred at every depth along each transect (Tables 9 - 12). These data also show that M. stellifera was the second most abundant species for all months.

The subtidal distribution of species, in terms of numbers of species, and the total densities for all species at each water depth along the transects are summarized in Table 14. In each instance there was an increase in the number

Table 9. Mean density/0.023 m^2 of *M. stellifera* faunal associates for subtidal transect, Jenness Beach, October 15, 1968.

Species (25)	Total No.	Depth (m) 0	1	2	3	4	5	7
Nematoda	171		3.0	36.0	25.5	11.0	10.0	3.0
Annelida								
Polychaeta								
Paraonis fulgens	21						9.0	1.5
Nephtys bucera	8							4.0
Phyllodoce mucosa	2							1.0
Scolelepis squamata	5	1.0	0.5					1.0
Mollusca								
Bivalvia								
Gemma gemma	71			5.5	2.5	23.5	3.0	1.0
Ensis directus	4							2.0
Siliqua costata	7						2.5	1.0
Mulinia lateralis	1							0.5
Gastropoda								
Lunatia heros	1							0.5
Arthropoda								
Tanaidacea								
Leptochelia savignyi	167			18.5	37.5	3.0	18.5	1.0
Isopoda								
Edotea triloba	12				1.0			5.0
Chiridotea tuftsi	9				1.0	2.0		1.5
Cumacea								
Leptocuma minor	193				43.5	2.5	9.5	41.0
Lamprops quadriplicata	20				0.5		3.5	6.0
Diastylis polita	72				0.5		4.0	31.5

Table 9, continued.

Species	Total No.	Depth (m) 0	1	2	3	4	5	7
Amphipoda								
Amphiporeia virginiana	8	4.0						
Bathyporeia quoddyensis	5589	367.0	636.0	597.0	485.0	592.5	116.0	2.0
Acanthohaustorius millsi	40	0.5	0.5	1.5	2.0	5.5	9.0	2.0
Protohaustorius deichmannae	218			0.5	3.0	12.5	68.5	26.0
Tryphosella sp.	37			1.0			17.5	
Unciola irroratus	17							8.5
Photis sp.	38						2.5	16.5
Anonyx sp.	1							0.5
Synchelidium sp.	22					1.0	3.5	6.5
Total Abundance	5969							
Total		372.5	640.0	660.0	602.0	651.5	288.0	173.5
Habitat Mean Density		93.1	160.0	94.3	54.7	72.4	20.6	7.5

Table 10. Mean density/0.023 m^2 of *M. stellifera* faunal associates for subtidal transect, Jenness Beach, January 12, 1969.

Species (26)	Total No.	Depth (m) 0	1	2	3	4	5	6
Nematoda	336		1.0	34.5	70.5	28.0	18.0	16.0
Annelida								
Polychaeta								
Paraonis fulgens	89			2.0	1.0	2.5	24.0	16.0
Nephtys bucera	3						1.0	1.0
Phyllodoce mucosa	2					0.5		0.5
Scolelepis squamata	4				0.5	0.5		1.0
Mollusca								
Bivalvia								
Gemma gemma	31				0.5		11.0	4.0
Tellina agilis	6					0.5	1.5	1.0
Siliqua costata	3						0.5	1.0
Mulinia lateralis	10			2.5	2.0		1.5	
Gastropoda								
Lunatia heros	1				0.5			
Nassarius trivittatus	1							0.5
Echinodermata								
Echinoidea								
Echinarachnius parma	1							0.5
Arthropoda								
Tanaidacea								
Leptochelia savignyi	197			3.0	23.5	14.0	26.0	31.5
Isopoda								
Edotea triloba	35					7.5	3.5	6.5
Chiridotea tuftsi	26			0.5	1.0	1.5	3.0	6.5

Table 10, continued.

Species	Total No.	Depth (m) 0	1	2	3	4	5	6
Cumacea								
Leptocuma minor	120				1.0	5.0	24.0	30.0
Lamprops quadriplicata	40				2.0	6.5	6.0	5.5
Diastylis polita	6						1.5	1.5
Mysidacea								
Neomysis americana	7					1.5	1.0	1.0
Amphipoda								
Amphiporeia virginiana	588	81.5	207.5	5.0				
Bathyporeia quoddyensis	7367	0.5	82.5	869.5	1183.0	698.5	364.5	485.0
Acanthohaustorius millsi	13		0.5	3.5	1.0			1.5
Protohaustorius deichmannae	352			1.0	20.0	20.5	33.0	101.5
Tryphosella sp.	2						0.5	0.5
Photis sp.	7						2.5	1.0
Synchelidium sp.	43					1.0	4.5	16.0
Total Abundance	9490							
Total		82.0	292.5	921.5	1306.5	798.0	523.0	729.5
Habitat Mean Density		41.0	73.1	102.6	100.5	57.0	27.5	31.7

Table 11. Mean density/0.023 m^2 of *M. stellifera* faunal associates for subtidal transect, Jenness Beach, March 16, 1969.

Species (22)	Total No.	Depth (m) 1	2	3	4	5	6
Nematoda	182	0.5	0.5	3.0	31.0	35.5	20.5
Annelida							
Polychaeta							
Paraonis fulgens	38				2.5	14.0	2.5
Nephtys bucera	8			0.5		1.5	2.0
Phyllodoce mucosa	4				0.5	0.5	1.0
Mollusca							
Bivalvia							
Gemma gemma	5						2.5
Tellina agilis	4					0.5	1.5
Siliqua costata	1					0.5	
Mulinia lateralis	1					0.5	
Echinodermata							
Echinoidea							
Echinarachnius parma	1					0.5	
Arthropoda							
Tanaidacea							
Leptochelia savignyi	56			1.0	17.0	7.0	3.0
Isopoda							
Edotea triloba	24				6.0	2.0	4.0
Chiridotea tuftsi	13	0.5	2.0		1.0		3.0
Cumacea							
Leptocuma minor	53		0.5		6.5	8.5	11.0
Lamprops quadriplicata	21		0.5	1.5	0.5	0.5	4.0
Diastylis polita	14						

Table 11, continued.

Species	Total No.	Depth (m) 1	2	3	4	5	6
Amphipoda							
Amphiporeia virginiana	212	18.5	13.0	74.5			
Bathyporeia quoddyensis	3579	19.5	41.3	75.0	794.0	207.0	653.0
Acanthohaustorius millsi	4					0.5	1.5
Protohaustorius deichmannae	372	0.5		1.5	74.5	62.0	47.5
Tryphosella sp.	3	1.0			1.0		
Photis sp.	3				1.0		0.5
Synchelidium sp.	23				1.0	0.5	10.0
Total Abundance	4621						
Total		40.5	58.0	159.5	949.0	342.5	770.5
Habitat Mean Density		6.8	8.3	79.9	67.8	20.1	45.3

Table 12. Mean density/0.023 m^2 of *M. stellifera* faunal associates for subtidal transect, Jenness Beach, August 30, 1969.

Species	Total No.	Depth (m) 0	1	2	3	4	5	6	7
Nematoda	169		8.5		15.5	3.0	12.0	16.5	27.5
Annelida									
Polychaeta									
Paraonis fulgens	149		4.5	2.5	6.0	14.5	12.0	19.0	16.0
Nephtys bucera	25					1.0		3.5	8.0
Phyllodoce mucosa	4							1.0	1.0
Scolelepis squamata	156		44.0	28.5	2.5	2.0		1.0	
Mollusca									
Bivalvia									
Gemma gemma	4						1.5	0.5	
Tellina agilis	7						1.0	0.5	2.0
Modiolus modiolus	1			0.5			0.5		
Ensis directus	1								
Mulinia lateralis	1								0.5
Gastropoda									
Lunatia heros	1								0.5
Echinodermata									
Echinoidea									
Echinarachnius parma	1							0.5	
Strongylocentrotus drobachiensis	77				0.5		7.5	9.5	21.0
Arthropoda									
Tanaidacea									
Leptochelia savignyi	132			6.5	38.0	3.5	10.5	6.0	1.3

Table 12, continued.

Species	Total No.	Depth (m) 0	1	2	3	4	5	6	7
Isopoda									
Edotea triloba	77	0.5		0.5	7.0	7.0	2.0	9.0	14.5
Idotea phosphorea	13			0.5	0.5	0.5		1.5	
Chiridotea tuftsi	37		3.5	0.5	7.0		3.0	2.0	6.0
Cumacea									
Leptocuma minor	142				3.0	6.0	12.0	18.0	32.0
Lamprops quadriplicata	16						3.5	2.0	2.5
Diastylis polita	128						5.0	26.0	33.0
Amphipoda									
Amphiporeia virginiana	295	83.0	63.0	1.0					
Bathyporeia quoddyensis	5968	72.0	978.0	627.0	607.0	451.0	138.5	104.5	6.0
Acanthohaustorius millsi	60		2.0	3.5	9.5	9.0	1.0	3.5	1.5
Protohaustorius deichmannae	626				37.5	3.5	40.5	126.0	105.5
Tryphosella sp.	210		1.0		102.5		0.5		0.5
Unciola irroratus	3							1.0	0.5
Photis sp.	61							20.5	10.0
Anonyx sp.	1							0.5	
Synchelidium sp.	123			2.0	0.5	2.0	4.0	16.0	37.0
Total Abundance	8487								
Total		155.5	1104.5	673.0	834.0	503.0	259.0	397.5	327.0
Habitat Mean Density		51.8	138.1	61.2	59.6	41.9	15.2	17.3	15.6

Table 13. Mean densities (no./0.023 m^2) of all species from four subtidal transects at Jenness Beach.

Species	Date of Transect 10-15-68	1-12-69	3-16-69	8-30-69
Nematoda	14.7	28.0	15.2	13.8
Polychaeta				
P. fulgens	5.2	9.1	6.3	10.6
N. bucera	4.0	1.0	1.2	4.5
P. mucosa	1.0	0.5	0.8	1.0
S. squamata	0.8	0.6		15.6
Bivalvia				
G. gemma	7.1	5.2	2.5	1.0
T. agilis		1.0	1.0	1.2
S. costata	1.7	0.7	0.5	
M. modiolus				0.3
E. directus	2.0			0.5
M. lateralis	0.5	1.8	0.5	0.5
Gastropoda				
L. heros	0.5	0.5		0.5
N. trivittatus		0.5		
Echinoidea				
E. parma		0.5	0.5	0.5
S. drobachiensis				9.6
Crustacea				
L. savignyi	15.7	15.7	7.0	11.0
E. triloba	3.0	5.8	4.0	5.8
I. phosphorea				1.6
C. tuftsi	1.5	2.5	1.6	3.1
M. stellifera	312.1	179.4	84.8	158.1
L. minor	24.7	15.0	6.6	14.2
L. quadriplicata	3.3	5.0	2.5	2.6
D. polita	12.0	1.5	1.2	21.3
N. americana		1.2		
A. virginiana	4.0	98.0	35.3	49.0
B. quoddyensis	399.3	562.2	298.3	373.0
A. millsi	3.0	1.6	1.0	4.3
P. deichmannae	22.3	35.4	37.2	62.6
Tryphosella sp.	9.2	0.5	1.0	26.1
U. irroratus	8.5			0.7
Photis sp.	9.5	1.7	0.5	15.2
Anonyx sp.	0.5			0.5
Synchelidium sp.	8.3	7.2	3.8	10.3

Table 14. Distribution and total densities of associated species for four Jenness Beach subtidal transects at times of low water.

Depth of Water (m)	Month October	January	March	August
0	4[1](372.5)[2]	2 (82.0)		3 (155.5)
1	4 (640.0)	6 (292.5)	6 (40.5)	8 (1104.5)
2	7 (660.0)	9 (921.5)	7 (58.0)	11 (673.0)
3	11 (602.0)	13 (1306.5)	8 (159.5)	14 (834.0)
4	8 (651.5)	14 (798.0)	14 (949.0)	12 (503.0)
5	15 (288.0)	19 (523.0)	17 (342.5)	17 (259.0)
6		23 (729.5)	17 (770.5)	22 (397.5)
7	23 (173.5)			20 (327.0)

1 - Number of species
2 - Total densities of all species

of species with increasing water depth. Greatest total densities occurred at 2 m in October, 3 m in January, 4 m in March and 1 m in August.

Per cent composition of the entire fauna for each transect according to taxa are shown in Table 15. Collectively, crustaceans constituted over 90% of the fauna for every season. Amphipods and cumaceans were the two most abundant crustacean orders, and M. stellifera alone accounted for 88 - 91% of the Cumacea for all months. Nematodes were outranked as the third most abundant taxon by polychaetes only in August, 1969. Echinoids and mysids were the least abundant taxa for the months when they were taken. Since mysids are primarily pelagic in habit, and since M. modiolus, N. trivattatus, S. drobachiensis, E. triloba, I. phosphorea and Photis sp. are essentially epifaunal species, these species should not be considered as components of the Jenness Beach subtidal infauna.

5. Plankton sampling

Data for Jenness Beach plankton samples are given in Table 16. Combined totals of 31 ovigerous females, 39 mature males and an estimated 16,694 immature specimens were collected in twenty-two tows made during nine different months, from 1968 to 1970. The majority of these tows were made during daylight hours in summer and early autumn in 1969.

The largest numbers of adults were collected on June 12 and July 24, 1969. The June 12 collection was made in strong surf, during daylight hours. The July 24 tow was taken in

Table 15. Per cent composition by taxa for four Jenness Beach transects. Column 1, M. stellifera included; column 2, M. stellifera omitted.

Taxon	October		January		March		August	
	1	2	1	2	1	2	1	2
Nematoda	1.60	2.49	2.94	3.62	3.29	3.94	1.61	2.01
Polychaeta	0.28	0.45	0.88	1.09	0.09	1.08	3.12	3.90
Bivalvia	1.04	1.62	0.45	0.55	0.20	0.24	0.16	0.20
Gastropoda	0.07	0.01	0.02	0.02	0.02	0.02	0.08	0.10
Echinoidea			0.01	0.01	0.02	0.02	0.73	0.91
Crustacea	(97.01)	(95.43)	(95.70)	(94.71)	(95.57)	(94.70)	(94.30)	(92.88)
Tanaidacea	1.31	2.04	1.72	2.12	1.01	1.21	1.27	1.60
Isopoda	0.15	0.24	0.53	0.66	0.67	0.80	1.25	1.57
Cumacea	37.65	3.62	20.26	1.79	18.15	1.90	22.49	2.86
Mysidacea			0.06	0.07				
Amphipoda	57.90	89.53	73.13	90.07	75.74	90.79	69.29	86.85
	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00

Table 16. Planktonic *M. stellifera* from Jenness Beach. Moon, N - first quarter, O - last quarter; surf, estimated surf zone wave height in feet; tide, F - flooding, E - ebbing.

Date	Time	Moon Light	Surf	Tide	Number of *M. stellifera*			
					Female	Male	Immature	Total
1968								
9-18	1300		1	F				0
10-15	1100		2	F				0
1969								
3-16	1600		2	F				0
4-26	1230		3	F		3		3
6-10	1030		1	E				0
6-12	1630		3-4	E	17	2	1	20
6-27	1400		2	E				0
7-24	2200	N	2-3	E	10	20	15400*	15430
7-28	0600		3-4	E		4	3	7
8-26	1600		0-1	E				0
9-6	2000	0	1	F			80	80
9-15	2300	N	3	F		2	1	3

Table 16, continued.

Date	Time	Moon Light	Surf	Tide	Number of *M. stellifera* Female	Male	Immature	Total
9-21	1400		2-3	F				0
10-2	0030	0	3-4	F				0
10-3	1230		3-4	F				0
10-17	1100		2-3	F	2	3	3	8
10-25	1900	Full	1	F			1160*	1160
11-18	1200		1	F			4	4
11-26	1900	N	1	F			4	4
12-21	1530		1	F				0
1970								
4-12	0930		1	E				0
6-14	0100	N	1	F	4	5	6	15

* Estimated number

relatively strong surf, under a cloudless, three-quarters full moon sky. Females outnumbered males by 8.5:1.0 on June 12, while on all other dates when adults were taken, males either outnumbered females, or males were the only adults taken. Adult animals were collected at night, under a new moon, or during the day in strong surf, but never during the day in calm surf.

The largest number of immatures were collected on July 24 and October 25, 1969. These tows were made on three-quarters and full moon nights, respectively. Collection numbers for July 24 and October 25 were estimated by subsampling. Careful examination of entire July 24 and October 25 samples showed that all of the specimens in these samples were manca larvae. Data for reproductive cycles at Jenness Beach (Fig. 10) show that percentages of ovigerous females were declining, while the percentages of immature individuals were increasing in July and October, 1969. These data suggest that brood release could have occurred on, or prior to, the days when these large numbers of manca larvae were collected.

The third largest collection of immatures at Jenness Beach (80) was made on September 6, 1969, under a waning moon and in calm surf. All of these specimens were either manca larvae, or unsexable juveniles. Unsexable individuals constituted all of the few immatures collected on all other dates.

Sixteen plankton tows were made in six different months during 1968 - 1970 at Little Harbor, N. H. (Table 17). Of the combined totals of one ovigerous female, ten mature males and four unsexable juveniles, only one female and one male were

Table 17. Planktonic *M. stellifera* from Little Harbor, N. H. Moon, N - first quarter.

Date	Time	Moon Light	Number of *M. stellifera* Female	Male	Immature	Total
1968						
3-11	1530					0
3-13	0800			3		3
3-13	2130	Full				0
3-24	1800					0
3-31	1100			4		4
12-11	1330				1	1
1969						
3-18	2130	New	1	1		2
3-19	0930			1		1
6-6	1500					0
6-21	1500					0
7-1	1030					0
7-25	0800			1		1
10-30	1100				1	1
1970						
4-4	0800					0
4-9	1200					0
6-14	0015	N			2	2

taken in one of the three night tows. Males were collected with greater frequency (five times) than females and immatures.

Mancocuma stellifera was not collected in fifteen plankton tows made at Dover Point during 1968 - 1969.

6. SCUBA Observations

SCUBA dives were made on June 11 and 12, July 17, 18 and 23 and September 16, 1969 in the area indicated in Figure 2. With the exception of June 12, a combination of gently breaking waves less than two feet in height, a moderate offshore wind, clear water and a cloudless sky produced ideal conditions for underwater observations at all depths. Accurate observations were possible only in deeper water on June 12, as three foot short period waves, produced by a strong onshore wind, created conditions that were unfavorable for surf zone observations.

The bottom was composed of fine sand throughout the area examined, and a regular pattern of wave-surge ripples extended from immediately beyond the surf zone to the deepest depth attained (4 m). No sand bars were observed, and only one oval-shaped boulder pavement, approximately fifteen feet in diameter, interrupted the regularity of the bottom. Large accumulations of detritus, composed primarily of fragments of brown and red algae, were found in the depressions between ripples on the June 12 dive. Only small, occasional clumps of this detritus were noted on all other dives. At no time were rip, or long shore currents detected.

A portion of each dive was devoted to observations directly within the surf zone, for the purpose of determining how the fauna reacted to, and how the substratum was affected by breaking waves. Few animals were seen uncovered by a breaking wave, even though many specimens of M. stellifera and the amphipods A. virginiana and B. quoddyensis were found whenever a handful of sand was overturned. The few cumaceans and amphipods exposed by wave action always reburrowed rapidly once a wave had passed. Only the uppermost layer of sand particles were carried into suspension by wave action, but they always settled out rapidly after a wave had passed. It should be noted, however, that these observations were made in relatively calm surf.

Mancocuma stellifera was found in abundance seaward of the surf zone on all dives. Hundreds of specimens emerged from the sand whenever the bottom was agitated by hand. Because of M. stellifera's mobility and sensitivity to disturbance of the substratum, no attempts were made to make in situ quantitative estimates. It was possible to actually see M. stellifera in undisturbed sand. This required considerable concentration, since the animals' small size, 2.0 - 3.6 mm, and brown-black color, tended to blend with the texture and color of sand particles. Generally, M. stellifera appeared to be rather evenly distributed in the depressions between ripples and on the crests and sides of ripples. From time to time, a specimen of M. stellifera emerged from the sand, moved a short distance and then reburrowed. Otherwise, there was little apparent activity on the part of M. stellifera, and at

no time, other than when I disturbed the sand, was M. stellifera seen to leave the bottom and swim toward the surface. When the sand was disturbed, it was possible to select and follow the movements of a single M. stellifera, from the time it emerged until it reburrowed. An animal usually responded by first swimming rapidly upward for a short distance and then sinking passively to the bottom. When it reached bottom, it would either burrow immediately, or scurry over the sand for a short distance prior to burrowing.

Negative results were obtained whenever the water column was examined for the pelagic presence of M. stellifera. This can be stated with confidence, since it was possible to see and follow the movements of small pelagic copepods.

A portion of each dive was also devoted to observations on the presence and activities of large infaunal and epifaunal associates. No attempt was made to count their numbers, but an estimate of the abundance of each species was recorded in a field notebook after each dive. Species which could not be identified at the time of each dive were captured and later identified in the laboratory. The results of these observations are summarized in Table 18.

7. Reproduction and Development

The results of reproduction and development studies are given in Table 19. A total of 62 precopula pairs were isolated, 33 in summer 1969 and 29 in spring 1970. Of these, five summer 1969 pairs held in isolation for four weeks failed to produce an ovigerous female; in two instances the female

Table 18. Faunal associate species observed at times of SCUBA dives at Jenness Beach. F, frequently observed; O, occasionally observed; R, rarely observed.

Species	Estimated Depth of Occurrence	Activities	Estimated Abundance
Crangon septemspinosus	Surf zone; low water line	Burrowed in sand	F
Neomysis americana	2–4 meters	Swimming in large schools close to bottom	O
Edotea triloba	Seaward of surf zone to 4 meters	Moving over bottom	O
Chiridotea tuftsi	"	"	R
Tryphosella sp.	All depths	Burrowed in sand	R
Lunatia heros	Seaward of surf zone to 4 meters	"	R
Pagurus longicarpus	Seaward of surf zone to 2 meters	Moving over bottom	O
Idotea phosphorea	Surf zone	Swimming in surf	F
Cancer borealis	2 meters	Buried in sand near boulders	O
Flatfish*	Seaward of surf zone to 4 meters	Swimming near bottom; lying on bottom; buried in sand	F

Table 19. Results of Reproduction and Development Studies.

	1969	1970
Number of Precopula Pairs Isolated	33	29
Range of Elapsed Time, Isolation to Brood Deposition (Days)	2-33	2-28
Average " " , " " " " "	11.9	16.9
Range of Elapsed Time, Last Molt to Brood Deposition (Hrs)	24-96	12-72
Average " " " " " " " "	38.8	18.6
Number of Females Molting Once Prior to Brood Deposition	27	28
" " " " Twice " " " "	1	1
Number of Females Molting, But Without a Brood	2	0
% Survival of Brooding Females for Entire Brooding Period	7.0	20.6
% Survival of Brood Removed from Dead Females	100	100
Range of Brooding Period, Surviving Females (Days)	52*	53-59
" " " " , Broods Removed from Dead Females (Days)	55-69	50-62
Average Brooding Period, Surviving Females (Days)	52*	54.7
" " " , Broods Removed from Dead Females (Days)	63.0	56.6
Number of Females not Molting and Without a Brood	3	0
Number of Males Molting	0	0
Temperature Range (^{o}C)	3-8	5-8

*Only one female survived the brooding period for the 1969 group.

molted once and the pair separated; in three instances the female did not molt and the pair remained in precopula for the entire isolation period. All of the spring 1970 pairs produced ovigerous females. In the majority of pairs, the female molted once prior to brood deposition. Only one female from each group molted twice before becoming ovigerous. None of the males molted, and in all instances, the male separated from the female, and it made no attempt to reassume the precopula position once the female became ovigerous.

The technique employed for maintaining healthy specimens was completely successful until females began to brood. All of the animals survived the precopula period, but, in spite of meticulous care, the mortality of brooding females was very high. Only two females survived in the 1969 group (6.0%) and only six females in the 1970 group (20.0%). On the other hand, survival of broods removed from dead females was 100% for both groups. The incubation periods for all broods are given in Table 19.

Relative to the temperature regime for these studies, it should be pointed out that an attempt was made to maintain all animals at the ambient habitat temperature. Faulty refrigeration equipment was used for the 1969 studies, and 8° C was the highest temperature attainable. In addition, the temperature frequently fluctuated between 3° and 8° C, whereas the habitat temperature during the study period ranged from 8.5° to 15.0° C. This factor must be taken into account when the results of laboratory incubation times for the 1969 group

are compared with development for the Jenness Beach population during summer 1969.

A Precision Scientific cold temperature incubator was used for the spring 1970 studies, and accurate temperature adjustments were therefore possible. The temperature for this work was gradually raised from 5° to 8° C, closely approximating the ambient habitat temperature during the study period.

All of the six females surviving the spring 1970 brooding period died within two weeks after brood release. None of these females molted, and only one had ripening gonads. No males were observed to assume the precopula position with these females.

On one occasion I was able to observe the actual deposition of eggs into the marsupium. At this time, I was routinely examining a recently molted female under the microscope. Accurate observations were possible, since the body of newmolts is quite transparent, and most features of the animal's gross internal anatomy are clearly visible. Individual eggs were distinguishable in the oviducts, and during the length of this observation (three-quarters of an hour) three eggs passed through the sternum of the third pereon somite into the marsupium. I did not see the openings through which the eggs passed, nor could I pinpoint the part of the sternum where the openings were located. This finding is in general agreement with the known location of the oviduct openings in other cumaceans, since Jones (1963) states that these openings are on the inner sides of the coxae of the third pereopods.

The examination of many embryos and newly released larvae throughout this investigation showed that M. stellifera's development is similar to the development described for other cumacean species (Sars, 1900; Zimmer, 1941; Corey, 1969). The stage at which the young cumacean emerges from the marsupium, the manca larva, is the only developmental stage studied in detail for M. stellifera. Figure 15 shows that M. stellifera's manca stage resembles the adult in most respects except for the lack of pigmentation and fifth pereopods.

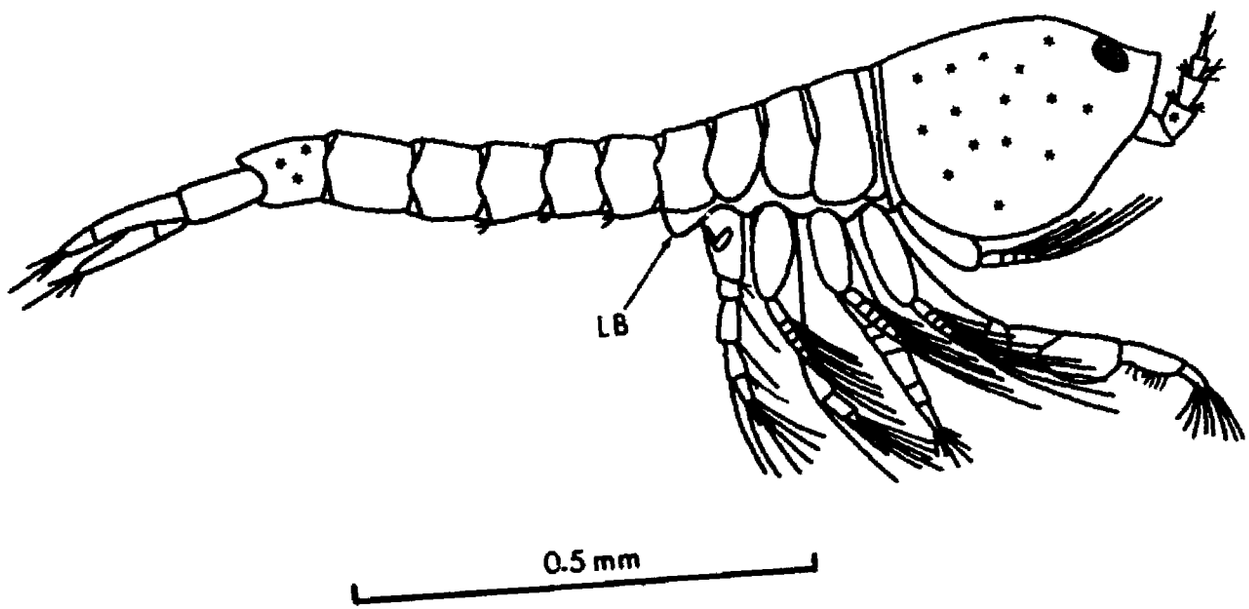
Negative results were obtained for attempts to rear specimens beyond the manca stage. None of the animals survived for more than a few days. Prior to dying, these juveniles appeared to be healthy and feeding, since many of them were observed to handle sand grains and detrital particles in the same manner described for the adults.

8. Behavioral Studies

a. Precopula and Copula

The study of precopula behavior in the laboratory was facilitated by the fact that the male's hold on the female is very tenacious; pairs rarely separated when they were transferred by pipette or when water in vessels containing precopula pairs was agitated during routine activities. In addition, males frequently retained their hold when precopula pairs were killed in preservative. The behavior of living specimens could therefore be studied with ease under a binocular microscope, and accurate camera lucida drawings could be made of preserved pairs.

Figure 15. Drawing of newly released M. stellifera manca larva. L B, limb bud of fifth pereopod.

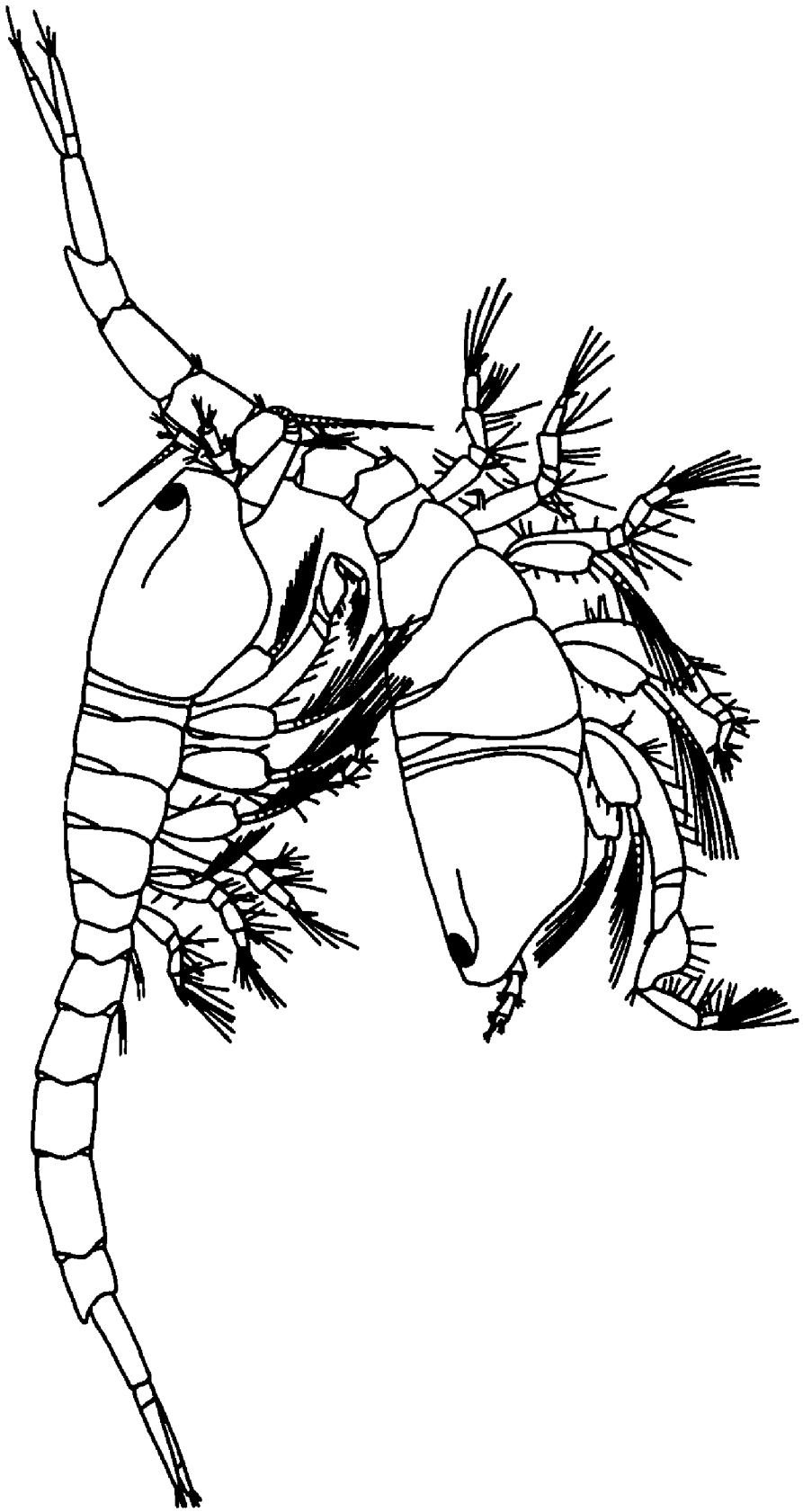

LB
0.5 mm

In the precopula position, the male utilizes the flagella of the second antennae as grasping organs to hold the female by her second or third abdominal segments. The animals face in opposite directions and the male's ventrum is opposed to the female's dorsum (Figs. 16 and 17). This position was maintained whenever precopula pairs were observed to swim, feed and burrow in the laboratory.

Swimming duties appeared to be shared equally by both sexes, with one member of the pair carried passively while the other swam. Only females were seen to burrow in the usual manner. At times of burrowing, males always maintained their grasp on females, and the male would often be buried head first and up to the anterior one-half of its abdomen. Males were never observed to assist in burrowing, and they were simply dragged along by the female whenever she moved through the sand.

It is difficult to say to what extent males feed during precopula. An examination of 40 freshly collected precopula pairs on March 12, 1970 showed that the intestines of 9 males were empty. Male members of pairs studied in the laboratory were never seen to handle sand grains or detrital particles, and males of pairs used for reproductive studies voided their intestines of fecal material shortly after being placed in isolation with a female. The intestines of these males remained empty as long as they continued to grasp females. On the other hand, females of precopula pairs were frequently seen to handle sand grains and detrital particles, and the

Figure 16. Drawing of M. stellifera in precopula. A, male; B, female.



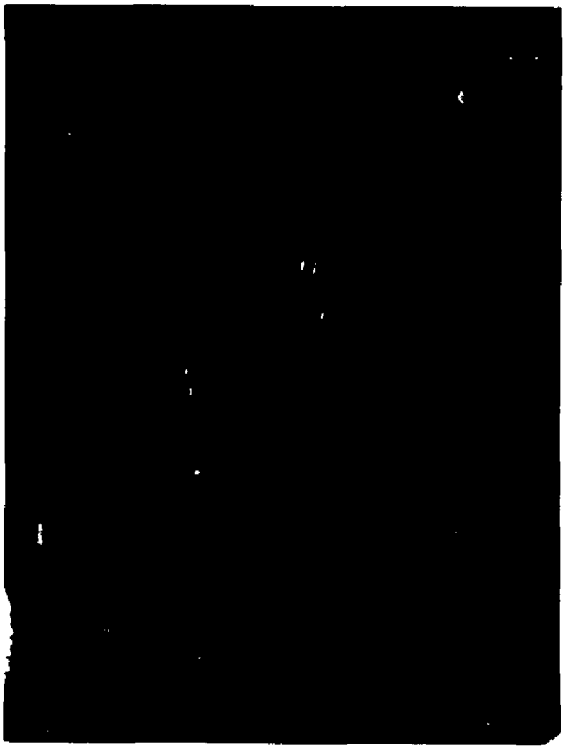


Figure 17. Polaroid photograph of M. stellifera in precopula. Female on the left; male on the right of the picture. (Courtesy of Dr. James M. Moulton, Dept. of Biology, Bowdoin College)

intestines of females used for reproductive studies were always full.

Collections of M. stellifera occasionally contained precopula pairs in which the female member was already ovigerous, and, males were occasionally seen to grasp males when large numbers of M. stellifera were placed together in a small vessel. In the latter situation, the pairs always separated shortly after they had joined. Concerning the former phenomenon, 115 precopula pairs were examined from a collection made on March 12, 1970. Of these, 98 females were non-ovigerous and 7 were ovigerous.

What was believed to be copulatory behavior was seen on one occasion. While observing a precopula pair from the spring 1970 group under a dissecting microscope, I noted that the female member appeared to be on the verge of molting, since her new exoskeleton was clearly visible beneath the old, transparent exoskeleton. In addition, the oviducts were filled with eggs and the marsupium appeared to be completely developed. The male grasped the female in the usual manner. The pair separated a few minutes after they were returned to their compartment, and re-examination of the female at this point under the microscope revealed that she had undergone ecdysis, as her exuvium was retrieved from the compartment. The female was again returned to her compartment, and shortly thereafter, the male began to swim rapidly and in a somewhat erratic manner. When the male came in contact with the female, lying quiescent on the bottom, he grasped her abdomen and the pair began to swim rapidly and in tight circles. During this

behavior, it appeared that the male repositioned himself so that the ventral surfaces of the animals were opposed to each other. I could not verify this last observation, since the animals were swimming too fast for me to make an accurate judgement. This activity continued for 30 to 40 second, then stopped as abruptly as it began, and the male released the female. I continued to observe the pair for an additional one-half hour, but the male made no further attempt to reassume the precopula position. When I examined the female under the microscope seventeen hours later, her oviducts were empty and her marsupium contained a brood.

b. Ecdysis

Ecdysis was observed for three females, with the following sequence of events taking place in all specimens. Initially, the carapace and first two thoracic segments were withdrawn from the exuvium through a split between the second and third thoracic segments. This separation was continuous from side-to-side, laterally and dorsally, but it did not extend through the ventral suture between the sternal plates of the second and third thoracic segments. The remaining thoracic segments were next withdrawn, followed by all of the abdominal segments. Once the first two thoracic segments were free, their pereopods were used to push the exuvium away from the posterior regions of the body. This process required one to two minutes, and the exuvium was shed in one piece.

c. Swimming

The general swimming behavior of animals in large

finger bowls containing sea water and sand was studied with the unaided eye for periods ranging from one-half to one hour at a time. Subsequently, animals were transferred to smaller vessels and viewed under a binocular microscope to allow observations of their activities at closer range.

Animals invariably swarmed at the point of greatest light intensity when they were first transferred from the holding refrigerator. This positive photactic behavior generally subsided with the passing of time, and most of the animals eventually settled into the sand, while a few continued to swim randomly. Burrowed animals occasionally emerged from the sand, swam for short distances and then reburrowed.

It was observed that M. stellifera swims rapidly and always in a forward direction. Although no attempt was made to measure swimming speeds, it was evident that males are the faster swimmers.

One of two reactions were observed whenever an animal came in contact with the water surface. In one, an animal stopped swimming, and as it began to sink, it assumed a horizontal position with the abdomen held upright at a 90^{o} angle to the thorax, the uropods extended, the first pereopods held outstretched and all other appendages retracted against the body. Sinking continued until the animal reached the bottom, or, swimming resumed after the animal had descended a short distance. In the other, an animal attempted to maintain its position at the surface by continued swimming.

Mancocuma stellifera employs two independent swimming methods. In the faster of the two, all pereopod and third

maxilliped exopodites are rotated, rapidly and in unison, the abdomen is extended posteriorly, with the uropods folded against each other, and all other appendages are tucked against the body. Because exopodite movement is faster than the eye, verification of their use was determined only after an animal had been narcotized by adding small amounts of magnesium chloride to the water. Swimming is the only apparent function of the exopodites, and when they are not in use, they are held against the endopodites. It was not determined whether or not the pleopods assist the male in swimming.

The abdomen is used in the other swimming method in the following way. With the uropods folded, it is first flexed forward beneath the thorax and then forceably straightened with the uropods extended. These movements are repeated in rapid succession, but they do not result in appreciable forward progression. In addition, they are never sustained for more than a few seconds at one time.

These observations concur, for the most part, with the swimming methods employed by other cumacean species (Foxon, 1936; Dixon, 1944). Dixon, however, concluded that Cumopsis goodsiri utilizes only the exopodites of the first pereopods when it swims in the first method described above.

d. Burrowing

The most efficient method for studying burrowing behavior consisted of first observing the activities of specimens in a small finger bowl containing sea water and sand under a binocular microscope set at its lowest

magnification. After most of the animals had burrowed, a single individual was isolated in the center of the field of vision at the next highest power. Gentle prodding with a dissecting needle usually induced the animal to emerge from the sand, move a short distance, and then reburrow, while remaining in the field of vision.

When burrowing commenced, the second to fifth pereopodal endopodites were used to scoop sand particles from beneath and to either side of the body. The animal sank into the depression created by this activity, and its body was covered by sand particles spilling over from the borders of the excavation. This procedure required only one or two seconds, and digging then stopped when an animal was either partially or completely buried. In the former position, the carapace and the first thoracic segment were exposed and held at a 45° angle to the substratum. In the latter position, only the tip of the carapace was exposed. In either position, the body was arched dorsally and the tips of the uropods often protruded above the surface.

Movement of burrowed animals was always seen to be directed forward, either directly forward or diagonally to the left. Forward progression was accomplished by the digging action of the pereopodal endopodites and the action of the abdomen, providing leverage by pressure of the uropods against the substrate when it was straightened.

e. Substratum Preference

The combination of sands used, and the results obtained

for substratum choice experiments are shown in Table 20. Preferences for sands, expressed as percentages, show that 1) unaltered (fresh) habitat sands were more attractive than treated sands, and 2) more animals preferred air-dried to acid-cleaned sands. Since the least numbers of animals chose acid-cleaned sands in every instance, these data suggest that soaking sand in concentrated sulfuric acid for 24 hrs was the treatment that rendered sands most unattractive to M. stellifera.

f. Food and Feeding

Accurate observations of M. stellifera's highly coordinated feeding activities could be studied best when an animal had assumed the partially buried position, since this position offered an excellent view of the feeding appendages, and since an individual would often remain stationary in this position for as long as twenty minutes at one time.

Fresh habitat sand grains were handled by starved animals in the following way. When the endopodite of the first pereopods were flexed inward at the joint between the ischium and the merus, sand grains caught by the expanded setae on the dactylus were transferred to and grasped by the endopodites of the third maxillipeds. Each grain was then rotated by the concerted action of all maxillipeds in such a manner that all grain surfaces were eventually oposed to the maxillipeds. Whether or not the maxillae and mandibles assisted in the action cannot be stated, as these mouthparts were hidden from view by the maxillipeds. A sand grain was retained for a few seconds to one-half minute, or it was rejected almost

Table 20. *M. stellifera* substratum preference experiments.

Treatment of Sand	No. Animals After 48 Hrs.	Percent Preference
Control		
Fresh Sand	123	61.5
Fresh Sand	77	38.5
Experiments		
Fresh Sand	146	73.0
Air-Dried Sand	54	27.0
Fresh Sand	166	83.0
Air-Dried, Acid-Cleaned Sand	34	17.0
Air-Dried Sand	146	73.0
Air-Dried, Acid-Cleaned Sand	54	27.0

immediately. In either case, a sand grain simply dropped in front of the animal once the grasp of the maxillipeds was relaxed. Discarded sand grains therefore tended to build up in front of an animal, if this activity continued for an extended period at one burrowing site. The first pereopods carried out their gathering activities only when the maxillipeds were free of sand grains, and they were held motionless when the maxillipeds were occupied.

A second, presumably feeding, activity of the first pereopods was frequently observed when sand grain feeding was not in progress. In this behavior, the pereopods were held in front of the body, well above the substrate and with the setae of the dactylus expanded. From time to time, the setae were swept through the water as the pereopods were alternately flexed at the joint between the carpus and propodus. This action stopped after several seconds, and each pereopod slowly drew its setae, again alternately, over the maxillipeds. At these times, the maxillipeds were seen to move rapidly, as if the setae were being cleaned of adherent particulate matter.

Starved animals accepted detrital offerings, as well as pieces of freshly dissected amphipods, isopods and cumaceans. These offerings were handled in the same manner described for sand grain feeding, or they were held stationary by the third maxillipeds while the second and first maxillipeds were worked against their surfaces. The latter method was used whenever softer material, such as animal flesh and pieces of algae, were handled.

In addition to these offerings, M. stellifera was also seen to handle its own fecal material, small living medusae and unidentifiable detritus.

Large ciliate protozoans were frequently present in fresh habitat sand used for feeding observations. At these times, the protozoans could be seen to move about on the surface of M. stellifera's carapace, antennae and maxillipeds, over the surface of sand grains and in the interstices between sand grains, all within range of the first pereopods. It is conceivable, therefore, that protozoans could be consumed during the course of M. stellifera's feeding activities, although their actual ingestion was never observed.

On two occasions several live nematodes found in fresh habitat sand were placed in front of burrowed animals, in close proximity to the third maxillipeds and first pereopods. At no time did M. stellifera attempt to grasp the nematodes, and, in one instance, a nematode was pushed aside by the first pereopods.

The gut contents of fifty specimens were examined microscopically during the course of this investigation. In all instances, these contents were unidentifiable detritus.

9. Predation

Two species, the sand shrimp, Crangon septemspinosus, and the smooth flounder Liopsetta putnami, preyed on M. stellifera under the laboratory conditions used for predation experiments. Negative results were obtained for all other species. Both the flounder and the shrimp consumed all twenty

specimens of M. stellifera in every experiment, and M. stellifera body parts always littered the bowl at the end of each shrimp experiment. It should be noted that predation occurred while the experimental bowls were kept in a dark refrigerator.

Observations of the predatory behavior of the shrimp and the flounder were made in daylight and at room temperature, when these predators were placed in a bowl containing 20 to 30 specimens of M. stellifera, sea water and sand.

Crangon septemspinosus captured M. stellifera with a high degree of accuracy by seizing specimens with its chelipeds. Few specimens eluded its grasp, and it often appeared that individuals were stalked prior to capture. The shrimp showed little apparent interest in swimming animals, as only burrowed individuals or individuals resting on the sand surface were captured. Once captured, M. stellifera was torn limb-from-limb as it was consumed. This feeding behavior on the part of the shrimp accounts for the body-part litter found in experimental bowls. All specimens of M. stellifera were usually consumed within one hour after an observation began.

When the flounder was placed in a bowl, it would first swim excitedly, gradually slow down, and then eventually come to rest on the bottom, either on the surface or burrowed in the sand. Both swimming and burrowing activities of the flounder forced many M. stellifera out of the sand, and a few of them would continue to swim for some time after the flounder had settled down. From time to time, the flounder would leave the bottom and swim slowly around the bowl to stalk swimming cumaceans. While at rest on the bottom, L. putnami consumed

swimmers whenever they ventured within range of the flounder's mouth. When swimmers were stalked, they were eaten while they were swimming or after they had come to rest on the bottom. In addition, while the flounder were swimming slowly around the bowl, it was seen time and again to single out and unerringly ingest burrowed individuals. As in the case of the sand shrimp, L. putnami consumed all M. stellifera within one hour after an observation began.

The stomach contents of five winter flounder (Pseudopleuronectes americanus), three old squaw ducks (Clangula hyemalis) and one smooth flounder (Liopsetta putnami) were examined (Table 21). Although M. stellifera was not found in the stomachs of any of these species, other cumacean species were present in stomach contents from old squaw ducks and the smooth flounder. The smooth flounder was collected from the Great Bay, N. H., estuary, and its feeding habits have no direct application to this investigation other than to indicate that this fish species consumes cumaceans. The cumaceans from the old squaws' stomachs, Leptocuma minor, Lamprops quadriplicata and Diastylis polita, are infaunal associates of M. stellifera and were collected at all seasons at Jenness Beach, from water depths of 3 - 7 m below low water levels (Tables 9 - 12).

The following observations were made on sea duck feeding activities at M. stellifera habitats. In November 1969 I observed a large raft of buffle-heads (Glaucionetta albeola) feeding at the time of low water in an estimated water depth of 2 - 3 m at Short Sands beach, York Beach, Maine. Mr. Henry

Table 21. Results of qualitative stomach analyses of potential predators on M. stellifera collected in the vicinity of the study area. Only cumaceans were identified to species.

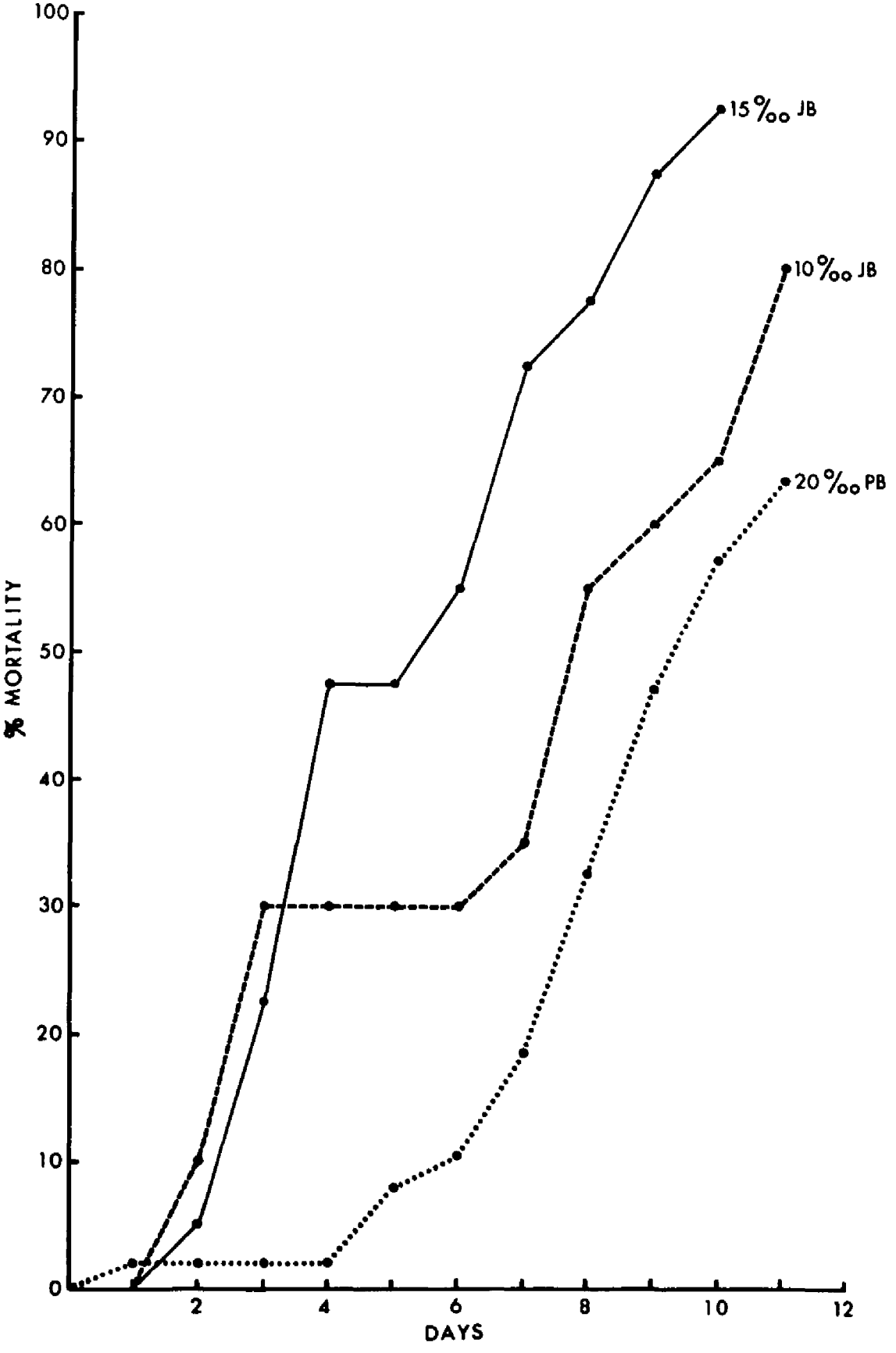
Species	Collector	Date & Location of Collection	Stomach Contents
Pseudopleuronectes americanus (Winter Flounder)	Weldon Bosworth	May, 1969; Steilman Rocks, New Castle, N. H.	Small snails Isopods Amphipods Small urchins Red and brown algae
Clangula hyemalis (Old Squaw Duck)	Richard Stott	Winter 1968-69; North Beach N. H.	Amphipods Leptocuma minor Diastylis polita Lampros quadriplicata
Liopsetta putnami (Smooth Flounder)	Phelps Laszlo	Summer 1969; Adam's Point Great Bay, N.H.	Amphipods Leucon americanus Oxyurostylis smithi

Tyler (personal communication) observed white-winged scoters (Melanitta fusca deglandi), surf scoters (Melanitta peris picillata), buffle-heads and American goldeneyes (Glaucionetta clangula americana) feeding directly in surf at Long Sands beach, York Beach, Maine, in 1969 and 1970.

10. Salinity Tolerances

The results of salinity tolerance experiments are inconclusive. At 5 °/oo, fifty per cent mortality occurred after only four hours. Fifty per cent mortalities for the other salinities (Fig. 18) were as follows: about 7.5 days at 10 °/oo, 5.3 days at 15 °/oo and 9.3 days at 20 °/oo. These data indicate that M. stellifera is not particularly euryhaline. Controls for each experiment showed 100% survival in "normal" sea water.

Figure 18. Salinity tolerance of Mancocuma stellifera. JB - Jenness Beach; each dot represents the mean of 40 animals (start). PB - Popham Beach; each dot represents the mean of 50 animals (start).


100
90
80
70
60
50
40
30
20
10
0
% MORTALITY
2
4
6
8
10
12
DAYS
15‰ JB
10‰ JB
20‰ PB

CHAPTER V

DISCUSSION

In reviewing the concept of marine bottom communities, Jones (1950) stressed the importance of the validity of samples, the methods of dealing with samples, the need for a close examination of species' life histories and density variations, and the influence of varying physical and biological factors on large assemblages of animals in the marine environment. By following Jones' (1950) guidelines, this study provided valuable information about the autecology of a dominant cumacean species, in addition to species diversity, density and zonation of inshore sand associations in the Gulf of Maine. Moreover, it was one of few in which the biology of a cumacean species was studied in depth for one or more years (Corey, 1969, 1970).

Holme (1954) discussed the various complex physical factors that influence the distribution of marine organisms, and pointed out that each may act at a different point in time in an individual's life history. In addition, he emphasized that some factors may be too subtle to detect by the usual means. Jones (1950) contended that the significant physical factors controlling the structure of marine benthic communities are temperature, salinity and the nature of the substratum. Although my work was primarily an autecological study, experimental laboratory and quantitative field data, correlated with field observations, permit certain conclusions concerning

environmental parameters that influenced the distribution and abundance of the cumacean M. stellifera in the subtidal sand community.

Concerning the physical nature of the substratum, Weiser (1959) attempted to correlate sand grain diameters with feeding habits and distributional patterns of small invertebrates at Puget Sound beaches. He suggested that critical grain sizes constituted distributional barriers, separating the major faunal components, and that size, rather than texture of the substrate exerts the most profound influence on the distribution of the fauna.

In regard to Weiser's hypothesis, a correlation could exist between subtidal sand grain diameters and M. stellifera's horizontal distribution. My granulometric data show that subtidal sand grain diameters decreased with increasing water depth of overlying water at all three habitats. Also, subtidal horizontal distribution of M. stellifera was similar at Jenness Beach, Wallis Sands and Long Sands. The main segments of these populations occurred at water depths of 0 - 4 m below low water levels. Seaward of 4 m, the substratum was composed of finer, silty sediments, and M. stellifera distribution was distinctly truncate. Whether or not M. stellifera's feeding appendages are morphologically adapted for manipulating sand grains within a specific sand grain diameter range is a matter of speculation, since I have no experimental data to support or refute this idea.

It is unlikely that annual salinity variations ever fall below M. stellifera's range of tolerance. My measurements of Jenness Beach surface waters show that annual salinities in 1968 and 1969 ranged from 28.0 to 34.0 °/oo. In 1968 - 1969 the average salinity was about 32 °/oo, well above the highest salinity that I used in tolerance experiments (20 °/oo). Fresh water runoff from Eel Pond and the salt marsh bordering Jenness Beach probably has little effect on Jenness Beach water, since fresh water flowing onto the beach in any volume would mix rapidly with sea water under the influence of wave action in the surf zone. In addition, fresh water seepage percolating through intertidal sands would have little effect on M. stellifera, since my data show that M. stellifera does not inhabit the intertidal zone. I did not find M. stellifera in my survey of the Great Bay, N. H., estuary. I did find M. stellifera in sands at the mouth of the Kennebec River (salinity 27.0 °/oo), but I did not determine how far M. stellifera penetrated up the river. Zimmer (1943) unfortunately did not include ecological data with his report on M. stellifera from the Matamek River. Bousfield (1962a) reported a salinity of 31.7 °/oo for the M. stellifera habitat in the Bay of Fundy.

Holme (1954), discussed the effect of surf on sand beach fauna, and stated that the depth of disturbance of surf zone surface sands is greatest on beaches with severe slopes and coarse sands. It will be recalled that Jenness Beach has a gentle slope and fine sands. Mancocuma stellifera were abundant in Jenness Beach surf zone sands at times of non-quantitative sampling, and surf zone SCUBA observations

indicated that surface sands are not appreciably disturbed by breaking waves. Knight-Jones and Morgan (1966) reviewed studies on pressure sensitivity of marine organisms, and suggested that cumaceans inhabiting surf zones utilize the undertow for seaward transport as an adaptive behavior to avoid harsh surf conditions. Jenness Beach is subject to extremely violent surf at times of coastal storms (personal observations), and the possibility that M. stellifera mortalities occur at these times should not be dismissed. Presumably, M. stellifera could avoid the stress placed on it by heavy surf by vertical burrowing or seaward migration.

Daily temperature variations probably have little effect on M. stellifera because of the species' subtidal habitat. Seasonal variations undoubtedly influence M. stellifera's reproductive cycles, growth and maturation. The effect of seasonal temperature variations on reproductive cycles of marine invertebrates is well documented (Kinne, 1963).

The extent to which lunar cycles might influence M. stellifera behavior is discussed below, in relation to sexual behavior.

Both Jones (1950) and Barnes (1969) considered the quality and quantity of food sources, predation, food chains, larval dispersal and interspecific competition as the more important biological factors of benthic and littoral ecology. Laboratory experiments, correlated with field observations, permit me to make more precise judgements about some of these biological factors, as they relate to the ecology of M.

stellifera. I will first discuss available food sources and M. stellifera feeding behavior.

Observations of feeding behavior demonstrated that M. stellifera is an epistrate feeder, and that its manipulation of sand grains is similar to the behavior reported for other cumaceans (Foxon, 1936; Dixon, 1944; Weiser, 1956). These observations also suggest that M. stellifera locates suitable food by plowing through surface sands, rather than by vertical burrowing or random search through agitated swimming. Food location could be accomplished by chemical tactile sense, rather than chemorecption at a distance (Gray and Johnson, 1970; discussed below).

Results of substratum preference experiments paralleled conclusions reached by other workers. Weiser (1956), investigating substratum choices by the cumacean, Cumacea vulgaris, found that untreated sands were preferred to dried sands. Meadows (1964) found that acid-cleaning and air-drying rendered sands unattractive to the amphipod Corophium arenarium, while Gray (1966) demonstrated that attractiveness of natural sands to the interstitial archiannelid Protrodrilus symbioticus was almost completely destroyed by acid-cleaning, heating, or drying at any temperature. Gray (1966) also reported that attractiveness of air-dried sands was almost completely restored after immersion in unfiltered sea water for 24 hrs, while attractiveness of acid-cleaned sands was only partially restored when they were subjected to the same treatment. He attributed these differences to a more rapid bacterial growth on air-dried sands. Considering my results, it is probable

that air-dried sands attracted more M. stellifera for similar reasons, since preference experiments ran for 48 hrs in unfiltered sea water.

A second possibility for the greater attractiveness of air-dried sands to M. stellifera should be considered. Meadows (1964) and Gray (1966) suggested that marine sands are covered with a primary organic film, defined by Gray (1966) as composed of extracellular secretions of micro-epiphytes and adsorbed organic molecules. Both workers believed that acid-cleaning destroyed this film. More recently, Meadows and Anderson (1968) and Gray and Johnson (1970) have demonstrated that marine sands lack an organic film. Rather, colonies of micro-organisms (bacteria, blue-green algae, diatoms, green algae and early stages of brown algae) occupy surface depressions, which are interspersed with smooth, bare surface areas (Meadows and Anderson, 1968). These latter workers emphasized, moreover, that these depressions represent well-defined habitats for the micro-organisms. It is therefore questionable if an unaltered organic film, in addition to bacterial growth, amplified the attractiveness of air-dried sands. A more plausible explanation would consider the destruction of micro-organisms by acid-cleaning, while micro-organisms' remains on air-dried sands promoted rapid bacterial growth. These questions will only be resolved by continuing work.

The greatest attractiveness of untreated sands to M. stellifera can logically be attributed to living micro-organisms. Microscopic examination of stained Jenness Beach sands (see Materials and Methods) showed stained patches only in surface

depressions, although no characteristic micro-organisms were distinguishable in the patches at the highest magnification used (X 930).

Weiser's (1959) study on sand grain size and distribution of sand-dwelling invertebrates was discussed above. The recent work of Gray and Johnson (1970) should be considered in relation to Weiser's hypothesis. In their study of the relation between marine sand bacteria and the ecology of an interstitial gastrotrich, Gray and Johnson (1970) demonstrated that the gastrotrich distinguished between sands containing different species of bacteria by direct contact (tactile chemical sense), rather than chemoreception at a distance. They concluded that tactile chemical response is of great importance in the ecology of sand-living meiofaunal species. They went on to point out that the species-distribution of bacteria present in marine sands is relevant to the distributional patterns of sand-dwelling macrofauna (polychaetes, amphipods, cumaceans) that are able to select narrow areas of an apparently homogeneous substratum in which they live.

Concerning responses to laboratory food offerings, it is reasonable to assume that plant and animal detritus are eaten by M. stellifera at times when this detritus is available. However, it is problematic whether or not M. stellifera preys on associated protozoans and small metazoans. Nicolaisen and Kanneworff (1969) studied the feeding behavior of the sand-dwelling amphipod Bathyporeia pilosa, and reported that B. pilosa, an epistrate feeder, did not respond to offerings of various species of interstitial ciliates or nematodes.

Since M. stellifera exhibited similar behavior, and since the feeding appendages of both M. stellifera and B. pilosa are modified for gathering and manipulating sand grains and small particles of organic detritus, rather than for seizing prey, it is doubtful if either of these species is predatory in habit.

Mancocuma stellifera's curious behavior of sweeping the first pereopods through the water, followed by drawing the setae over the mouthparts (heretofore unreported for cumaceans) might suggest that the animal employs a type of filter feeding habit. However, since the pereopod setae are non-plumose, it is improbable that they function as effective straining devices in the extraction of particulate matter or microplankters from water. This behavior remains unexplained.

In view of the foregoing discussions, it is proposed that the two primary energy sources for M. stellifera are, in order of magnitude, sand grain micro-organisms and organic detritus. I suggest that, although the effect of grain size itself (Weiser, 1959) on either abundance or distribution of M. stellifera is a distinct possibility, the species-distribution of sand grain micro-organisms (Gray and Johnson, 1970) should be investigated before final judgements are made about factors controlling the distribution of M. stellifera.

Data concerning predation on cumaceans are few. Jones and Burbanck (1959) reported the brackish water cumacean, Almyracuma proximoculi, from stomachs of small American eels, and suggested that other small fish, shore birds and ducks also feed on A. proximoculi. Jones (1963) stated that fish eat cumaceans, but he did not support this with specific references.

Edwards and Steele (1968) found sand-dwelling cumaceans in stomachs of plaice and dab at Loch Ewe, Scotland, and Johnson (1969) reported cumaceans were the largest component of food for a subtidal snailfish in California waters.

My laboratory experiments showed that sand shrimp and flatfish will eat M. stellifera under controlled conditions. Although these data are circumstantial, they do provide information on the predatory behavior of C. septemspinosus and L. putnami. C. septemspinosus was able to locate and consume burrowed M. stellifera in daylight and in the dark. The flatfish stalked swimming prey, and easily recognized burrowed animals. It is probable that similar predation occurs in the field.

More positive proof of predation on cumaceans in the field was obtained from diving duck and flatfish stomach analyses. Stomach contents from the Great Bay flatfish contained two cumaceans that I have collected from Great Bay mudflats and sandflats, Leucon americana and Oxyurostylis smithii. Old squaw stomach contents contained three cumaceans species that were consistently collected at the outer distributional boundary (5 - 7 m) of M. stellifera at Jenness Beach. My field observations of diving duck feeding activities at New Hampshire and Maine beaches showed that these birds do feed in surf zone and shallow subtidal water on occasions. Also, flatfish were observed on subtidal sands (SCUBA observations), and C. septemspinosus was found relatively abundant in shallow water at times of low tide at Jenness Beach in summer 1969. It is therefore reasonable to assume that M.

stellifera and other subtidal infauna constitute part of the diet of these animals.

Mills (1967), discussed predation by shorebirds on sandflat amphipods (Ampelisca) at Barnstable Harbor, and concluded that amphipod mortality due to shorebird feeding must be heavy at times. I have observed shorebirds feeding on Jenness Beach at low water levels, during times of spring tides. At the same time, I found large numbers of M. stellifera at the very edge of the water. These M. stellifera were often stranded by receding waves. Predation by shorebirds at times of spring tides should be an additional factor to consider in the regulation of M. stellifera densities.

It has long been known that the planktonic stages of littoral organisms, such as barnacles, may be dominant food for some fishes (Barnes, 1969). The extent to which the juvenile stages of sand beach crustaceans are utilized as food by plankton feeders is unknown. Mauchline (1967) suggested that predation by inshore fish was significant in reducing the very large juvenile population of mysids at sandy bays in Scotland. Watkin (1941) reported that juvenile stages constituted 40% of the cumacean, Pseudocuma cercaria, collected in night plankton tows at Kames Bay, Scotland. Juveniles constituted over 90% of M. stellifera collected in night tows at Jenness Beach. The greatest estimated number of juveniles taken in any one night tow was 15,400, as compared to a maximum of 259 for P. cercaria (Watkin, 1941). Plankton data suggest that juvenile M. stellifera are pelagic in habit after leaving the female marsupium. If this occurs, and if plankton feeders

consumed M. stellifera juveniles, then significant juvenile mortalities would occur when new generations entered the M. stellifera population.

Although the foregoing discussion has distinct implications relating to density regulation of M. stellifera by predation, experimental data and field observations do not permit any more definite conclusions. However, I believe predation should be considered as an additional factor contributing to M. stellifera density variations at Jenness Beach during 1968 - 1969.

Density estimates for M. stellifera and other macrofauna indicate that Jenness Beach subtidal sands produce a considerable biomass volume annually. Since M. stellifera ranked second in dominance among the fauna, and since this biomass is undoubtedly exploited by higher trophic levels, then M. stellifera most probably plays a significant role in the energy exchange of the Jenness Beach ecosystem.

I have no evidence upon which to draw conclusions regarding competition for food and space between M. stellifera and its faunal associates. However, seasonal overlaps occurred at M. stellifera's outer distributional limits (4 - 6 m) and the horizontal distributions of three other cumaceans, L. minor, L. quadriplicata and D. polita. Of these three species, only L. minor overlapped considerably with M. stellifera, but L. minor's densities were always considerably lower than M. stellifera densities. Also, the densities of these cumaceans increased while M. stellifera densities decreased with depth of overlying water during each season.

Bathyporeia quoddyensis, the numerically dominant infaunal species at Jenness Beach for all seasons, could be M. stellifera's greatest competitor, since B. quoddyensis maximum densities generally coincided with the depth distribution of M. stellifera maximum densities. Unfortunately, no information is available on the biology of B. quoddyensis (Dr. Robert Croker, personal communication). Nicolaisen and Kanneworff (1969) studied the burrowing and feeding behaviors of two sand-dwelling species of Bathyporeia from Danish waters, B. sarsi and B. pilosa. Nicolaisen and Kanneworff (1969) reported that these amphipods burrow into sand to depths of several cm, and that they are epistrate feeders, apparently utilizing the micro-organisms on sand grains as food sources. If B. quoddyensis has similar burrowing and feeding behaviors, then it is apparent that B. quoddyensis and M. stellifera occupy closely spaced strata in subtidal sands, and possibly exploit similar food sources. In the field (SCUBA observations), I always distinguished M. stellifera in surface sands, but I rarely saw amphipods in these same sands. Amphipods were generally easy to detect if present, because their white body color contrasted sharply with the dark sands. On the other hand, I always found abundant A. virginiana and B. quoddyensis whenever I disturbed the upper few cm of surface sands. It is intriguing to speculate about B. quoddyensis and M. stellifera burrowing and feeding behavior differences, as well as discrete differences between the micro-organisms on surface and sub-surface sand grains, that would account for the closely spaced

zonation of M. stellifera and B. quoddyensis. It is equally intriguing to speculate about the environmental factors that would account for the observed zonations of M. stellifera and the other three cumacean species.

To summarize, some of the more obvious physical and biological factors presumably influencing the density and distribution of the M. stellifera population at Jenness Beach were discussed. I will now consider M. stellifera zonation, density and population changes, and sexual biology, concluding the discussion with considerations of the associated macrofaunal species.

The following picture of M. stellifera zonation at Jenness Beach has emerged from this study. The main segment of the population inhabitated the upper layer of subtidal sands from water depths of 1 - 5 m below low water levels, where median sand grain diameters measure between 0.348 and 0.166 mm, respectively. No significant changes in the population's horizontal distribution occurred by season, horizontal segregation of sexes was not evident, and the population did not migrate onto intertidal sands at times of flooding tides. The occurrence of juveniles at outer water depth distributional limits (5 - 7 m) at the three habitats samples is discussed below, in relation to larval dispersal. Similar data on M. stellifera horizontal distribution at Wallis Sands and Long Sands presented additional evidence that M. stellifera zonation at Jenness Beach was real. It is concluded that M. stellifera is a subtidal species with only limited penetration above MLW (0.0) level. The Jenness Beach M. stellifera

population is therefore an ecological unit, including all life stages, with the subtidal environment at Jenness Beach possessing characteristics, some of which are still obscure, that account for the species' distributional pattern.

The only comparable data for other cumaceans were reported by McIntyre and Eleftheriou (1968) and Corey (1970). McIntyre and Eleftheriou (1968) found that three cumaceans showed distinct zonation at water depths of 1 - 10 m below low water spring tides on subtidal sands at Firemore Bay, Scotland. Corey (1970) reported similar results for two cumaceans at Kames Bay, Scotland, and found that these species inhabitated sublittoral sands from MLWS to water depths where sands began to grade into mud (no depths reported). Moreover, Corey (1970) concluded that these cumaceans did not migrate into littoral sands with flooding tides.

Data on abundance and density show that M. stellifera was the second dominant subtidal macrofauna species at Jenness Beach during 1968 and 1969. A low ($\pm$ 13.3) average coefficient of variation for Jenness Beach M. stellifera habitat mean densities, ranging from 69.6 - 312.1/0.023 m^2, and the fact that the distribution of the main segment of the Jenness Beach M. stellifera population was consistent during 1968 - 1969 indicate a reliable sampling design. I have extrapolated my greatest M. stellifera mean density (916.5/0.023 m^2) to give a theoretical M. stellifera density for a sample area of 0.1 m^2. This theoretical value is presented in Table 22, along with maximum cumacean densities, adjusted to sample areas of 0.1 m^2, from other locations. Accordingly, Table 22 shows

Table 22. Density estimates of cumaceans from subtidal sands at various locations.

Location	Mesh Size (mm)	Reported Sample Area	Water Depth Range	Greatest Density ($\bar{x}$) ($0.1\ m^2$)
Jenness Beach, N. H. (This Thesis)	0.25	0.023 m^2	0 - 7 m	3986.8
Washington Coast (Lie, 1969)	1.00	1.0 m^2	12 - 155 m	1449.3
Kames Bay, Scotland (Corey, 1970)	0.20	0.1 m^2	Shallow Subtidal (No Depths Reported)	272.0
Firemore Bay, U. K. (McIntyre and Eleftheriou, 1968)	0.50	1.0 m^2	1 - 6 m	16.7
Puget Sound, Wash. (Lie, 1968)	1.00	1.0 m^2	10 - 18 m	14.7
So. California Coast (Barnard, 1963)	0.50	1.0 m^2	2 - 5 fm	10.1
Frustration Bay, Can. (Ellis, 1960)	2.00	1.0 m^2	5 m	6.7

that Jenness Beach density ranks first. Lie (1969) (Table 22) did not give depthwise densities for his Washington coast data, so I do not know at which depth his greatest density, 14,493/m^2, occurred. Otherwise, my estimate is about fifteen times greater than the Kames Bay estimate, and about six hundred times greater than the Frustration Bay estimate (Table 22). Further extrapolation of the same M. stellifera density estimate for a sample area of 1.0 m^2 gives a theoretical value of 39,868 M. stellifera/1.0 m^2. To my knowledge, the only other density estimates for sand-dwelling crustaceans that surpass it are those reported for the intertidal amphipod Bathyporeia pilosa, 60,000/1.0 m^2 (Nicolaisen and Kanneworff, 1969), and my theoretical estimate for Bathyporeia quoddyensis, 51,460/1.0 m^2, derived by extrapolating B. quoddyensis' highest Jenness Beach density estimate (1183.0/0.023 m^2, January 1969).

The correlations between M. stellifera density changes and reproductive cycles were discussed earlier. The data did not reflect a significant increase in population density in June 1969, while reproductive cycle data showed increased reproduction at this time. The following factors should be considered as possible reasons for any discrepancies. 1) High rates of natural mortality for older members of the population, coupled with increasing summer predation on the population, probably occurred concurrently with the entrance of the new generation. 2) Because of larval dispersal (discussed below), most juveniles of the summer generation might have been inhabiting sands at depths greater than 7 m, and therefore would not have been collected in samples for

reproductive cycle data (0 - 1 m) and density changes (0 - 7 m). 3) Brood releases occurred gradually, not within a closely spaced time period, and population density did not increase significantly at any one time. 4) The samples for reproductive cycle data (June 1), and the June transect (June 17) may have been taken before the main segment of the new generation entered the population.

Otherwise, the overall density changes of M. stellifera at Jenness Beach during 1968 - 1969 can be summarized as follows. Increasing natality in summer accounted for density increases in summer and early fall, with peak density occurring at the time of the production of the fall generation. Decreasing natality and higher natural mortality in late fall, over winter and into early spring resulted in density decreases, with lowest density occurring after spring breeding.

Fecundity and sex ratio data showed that M. stellifera's biotic potential, defined by Andrewartha and Birch (1954) as an organism's innate capacity for maximum growth under ideal conditions, was highest in summer than at any other time in 1969. High fecundity is here interpreted as high reproductive potential, and increasing numbers of females compared to males occurred in the population from spring to late summer, insuring high frequencies of fertilization. Increasing fecundity from May through September 1969 correlated with increasing 1969 summer density estimates. By assuming that the September and October 1969 density estimates (no data obtained) would have been similar to the September and October 1968 density estimates, it may be concluded that maximum

population growth occurs at the end of summer, when the fall generation enters the population.

There was a correlation between the annual water temperature variations at Jenness Beach and M. stellifera's reproductive cycles in 1969. Spring breeding occurred when the water temperature was about 4° C. Reproduction increased as water temperature increased during summer, and reached a maximum in September 1969 when water temperature was about 16° C. Reproduction, growth and maturation decreased during fall and winter 1968 - 1969, as water temperature decreased from about 18° C to about 2° C, respectively. Similar correlations were reported for other Atlantic boreal peracaridians: Amphipoda (Sameoto, 1969a; Fish and Preece, 1970), Isopoda (Fish, 1970; Jones, 1970), and Mysidacea (Mauchline, 1965, 1967, 1969).

Corey (1969), reviewed studies on cumacean reproductive cycles, and reported that the life history of only one species, Diastylis rathkei, had been worked out prior to his study of the life histories of three sand-dwelling Atlantic boreal cumaceans, Cumopsis goodsiri, Iphinoe trispinosa and Pseudocuma longicornis. Both C. goodsiri, an intertidal species, and I. trispinosa, a subtidal species, produce two distinct generations per year, one in early summer, the other in late summer. Iphinoe trispinosa's late summer generation is reinforced by additional recruitment in late fall. Pseudocuma longicornis, a subtidal species, reproduces continuously throughout the year, but does not produce distinct generations at any time. Corey (1969), correlated information compiled by Zimmer (1941)

on cumacean reproductive cycles with his work, and concluded that most littoral species probably breed twice per year, while most deep water species breed only once per year, in winter months. Reproductive data for M. stellifera are in agreement with the life cycles reported for I. trispinosa and other subtidal cumaceans (Corey, 1969). Therefore, I am not convinced that M. stellifera produces a third distinct generation in winter, as shown by length frequency data. More likely, M. stellifera's life cycle is similar to I. trispinosa's life cycle, with the individuals that I have designated as the winter generation representing late fall recruitment and slow growth during winter. Only continuing work on M. stellifera's reproductive cycles will resolve this question.

I have relatively little data regarding the length of embryonic development for M. stellifera by season. Laboratory studies showed that M. stellifera incubation periods were about 52 days in summer 1969 and about 55 days in spring 1970. Corey (1969) reported that development within the marsupium for C. goodsiri and I. trispinosa took one month in summer and two months in winter. Spring 1969 incubation studies on M. stellifera were conducted at water temperatures ranging from 5° - 8° C, approximating ambient habitat temperatures. Thus, I can safely conclude that M. stellifera development takes about two months in spring. Summer 1969 development data do not permit any conclusion in regard to the length of M. stellifera summer development, since this work was carried out at temperatures well below the ambient habitat temperatures, about 3° - 8° versus 13° - 16° C, respectively.

Mancocuma stellifera longevity appears to differ between sexes, i.e., 6 - 7 months for males and 10 - 11 months for females, but differences between longevities of generations were not apparent. These data conflict with conclusions reached by Corey (1969), who reported that the maximum life spans of C. goodsiri and I. trispinosa were equal for sexes, but different for each generation, 5 months for summer animals and 12 months for winter animals.

The longer life span of female M. stellifera accounts for the occurrence of non-ovigerous females that were larger than ovigerous females in a given population sample. It also infers that females produce several broods during their life span. I believe that female M. stellifera reproductive patterns occur in the following sequence. The first molt following brood release results in the loss of oostegites. New oostegites are regenerated during successive molts, and a new marsupium eventually reforms. Shortly thereafter, the female mates and produces a new brood. This pattern was inferred from my examination of many relatively large non-ovigerous females during all seasons. These females bore oostegites and ovaries in various stages of development, and they were usually larger than brooding females collected at the same time.

To my knowledge, laboratory observations of M. stellifera sexual behavior revealed two phenomena thus far unreported for Cumacea. Mancocuma stellifera precopula behavior was similar to reports for other cumaceans (Zimmer, 1941), in regard to the male's use of the second antennae as a grasping organ. It differed in regard to the male and female facing

in opposite directions. Concerning copulation, the secretion of a male attracting pheromone by the female immediately following molting could be responsible for the attendant male's excited behavior prior to copulation. Clutter and Theilacker (1971) reported that copulation of pelagic mysids occurs within two or three minutes after the female molts, and apparently only when the female exudes a pheromone to attract adult males of the same species.

Correlations between swarming in surface water, for the purpose of achieving mating contacts, and lunar cycles were reported for cumaceans (Jones, 1963) and for amphipods (Mills, 1967; Fincham, 1970). I have little evidence to support the possibility that M. stellifera has a similar mating behavior. Since M. stellifera densities within relatively restricted subtidal areas were shown to be high at the three habitats sampled in summer 1969 and 1970, and since large numbers of M. stellifera in precopula have been observed in sands at low water levels during breeding seasons (personal observations; Dr. Robert Croker, personal communication), I believe that M. stellifera achieves mating contact through movement over the substratum, rather than swarming in surface waters. However, my plankton data are inconclusive in this regard, and additional field and laboratory studies are needed before this question can be resolved.

Regarding collections of large numbers of M. stellifera manca larvae in night plankton tows, Mauchline (1967) suggested that the intensity of moonlight was one factor influencing diurnal vertical migrations of juvenile mysids at Lock Ewe,

Scotland. Watkin (1941) collected more juvenile cumaceans in night plankton under full moons than at other times, and Corey (1969) found that newly released juvenile C. goodsiri were frequently found swimming. Corey (1969) contended that the tendency of juveniles to swim, rather than settle, aids in the dispersal of the young. I believe that young M. stellifera have similar behavior, as follows. Upon leaving the marsupium, manca larvae are benthic by day and pelagic by night. Their pelagic behavior could be in response to population pressure, lunar cycles, an adaptive behavior for plankton feeding, or for colonizing substrata better suited to their feeding habits, i.e., finer sands containing large quantities of organic detritus. This behavior would account for abundant manca larvae in plankton samples and in transect samples from water depths of 5 - 7 m in summer 1969 and 1970. My plankton data show that their tendency to swim is greatest during new moons of lunar cycles, and it is at these times that dispersal of the larvae (juveniles) is greatest.

There are few data on the eastern Atlantic boreal shallow water sand associations (McIntyre and Eletheriou, 1968; Fincham, 1969; McIntyre, 1970), and there is only one published report on these associations in the western Atlantic (Sameoto, 1969b). Accordingly, the following discussion about M. stellifera macrofaunal associates is based on personal communications with Dr. Robert Croker concerning his unpublished data.

Changes in the abundance of A. virginiana and B. quoddyensis substantially affected total abundance of the

Jenness Beach subtidal infauna. Croker's intertidal data indicate fewer A. virginiana intertidally during winter months, as compared with summer and early fall. These seasonal differences are dependent upon beach slope, apparent movement of the population subtidally and other factors as yet unknown. Also, for A. virginiana, there is an increase in the per cent of juveniles in the population from about June to a peak in October. There is also a good indication of a correlation of size (and age) with position on the beach and below the low water line for A. virginiana, i.e., smaller and younger animals, and males (smaller than females) are increasingly abundant on the lower beach and subtidally. It should be pointed out that A. virginiana has a somewhat looser infaunal association than many of the other infaunal species; its planktonic presence is presently under investigation.

The biology of B. quoddyensis, the numerically dominant subtidal species among the infauna at Jenness Beach, has not been studied. Croker has not found B. quoddyensis intertidally except in small numbers just above and below MLW (0.0) level, and Sameoto (1969b) reported an unidentified Bathyporeia sp. from subtidal sands only, at Nobska Beach, Cape Cod. Hence, little can be said about B. quoddyensis, other than it is a subtidal species, and that its seasonal densities and zonation overlapped those of M. stellifera.

In regard to A. millsi, the data are opposite from what would be expected, since the species was least abundant in the winter subtidally, when it is generally low in abundance or absent in the intertidal zone (Sameoto, 1969b). Croker

believes that part of the answer is that A. millsi distribution must continue deeper than my transect depths (Table 10). A. millsi densities in January 1969 (Table 10) could then be viewed as composed of stragglers from deeper waters.

In any event, Croker's data show that A. virginiana and A. millsi are two species that occur commonly in the lower half of the intertidal zone during warmer months.

In summary, my work indicates that four common Gulf of Maine intertidal sand species extend subtidally (A. millsi, Tryphosella sp., A. virginiana and S. squamata), and that three other species found subtidally at Jenness Beach are found in Gulf of Maine intertidal sands during warmer months (C. tuftsi, N. bucera and P. fulgens) (Croker, personal communication).

Since B. quoddyensis and M. stellifera were codominant species of the Jenness Beach subtidal infauna at water depths of 0 - 5 m below low water levels, and since M. stellifera was not a conspicuous member of the infauna at subtidal water depths greater than 5 m, it is proposed that near shore subtidal sand associations of the western Atlantic boreal region, possessing physical and biological characteristics similar to Jenness Beach, be characterized as Bathyporeia - Mancocuma associations.

In conclusion, McIntyre (1970), discussing the reasons for his study of the range of biomass in intertidal sands, stated, "A need is being increasingly felt for more basic data on the structure of animal communities in unpolluted coastal water, and on the range of natural variation within

these communities so that base lines can be set, against which changes due to pollution may be assessed." Accordingly, my work may be of some value in future years, should the relatively pristine Gulf of Maine beaches ever become polluted.

CHAPTER VI

SUMMARY

1. Mancocuma stellifera Zimmer, 1943 is redescribed. Figures of the species and a report of its occurrence from the continental United States are presented for the first time. Mancocuma stellifera's known geographical range is from the Gulf of St. Lawrence to Cape Ann, Massachusetts. Data in this thesis indicate that the species should be included with the western Atlantic boreal fauna, and as a member of the infauna of nearshore subtidal sands.
2. A population of M. stellifera at Jenness Beach, Rye Beach, N. H., a semi-exposed beach with a gentle slope and clean compact sands, was sampled quantitatively with an Ekman dredge (0.023 m^2) from July 1968 through December 1969. Monthly samples provided data on reproductive cycles and changes in population composition, while seasonal subtidal transects provided data on population density variations and zonation. Laboratory studies included experiments concerning behavior, predation and salinity tolerances.
3. Reproduction was continuous throughout 1968 and 1969, but at lowest intensities in fall and winter. Annual breeding cycles commenced in spring and peaked in late summer, when surface water temperatures were about 4° and 16° C, respectively. Fecundity and sex ratio data showed that biotic potential was greatest in late summer. Two distinct generations entered the population annually, in mid-summer

and early fall. Females produced two or more broods annually, estimated incubation periods were one month in summer and two months in winter, and estimated maximum life spans were 7 months for males and 11 months for females. Seasonal habitat mean densities ranged from a maximum of 312.1/0.023 m^2 in fall to a minimum of 69.6/0.023 m^2 in spring. Analyses of these data showed that maximum population growth occurred when the fall generation entered the population.

4. Seasonal subtidal transects showed that M. stellifera inhabited subtidal sands at water depths of 0 - 7 m below low water levels, and that the main segment of the population occurred at water depths of 1 - 5 m, where mean sand grain diameters ranged from 0.385 to 0.166 mm, respectively. Similar results were obtained for subtidal transects at Wallis Sands, Rye Beach, N. H., and Long Sands, York Beach, Me. The Jenness Beach population did not occur on air-exposed sands or migrate onto intertidal sands on flooding tides. No significant differences in zonation occurred by season or sexes, although small juveniles and manca larvae comprised 73 - 95% of the population at water depths of 5 - 7 m during reproductive periods. It was concluded that the Jenness Beach population functioned as an ecological unit including all life history stages.
5. The position assumed by M. stellifera during precopula was figured and considered as unique for Cumacea. Mating occurred after the final female precopula molt, and mating behavior suggested that a male-attracting pheromone might

play a significant role in copula. During ecdysis, the exoskeleton was shed as one piece. The female marsupium was shed and reformed during successive postbrooding molts.

6. Mancocuma stellifera exhibited typical cumacean development. Embryos were incubated in the marsupium and development terminated in a free-living manca larval stage. The manca larva was figured, and excised embryos were successfully reared with a minimum of care.
7. Correlation of in situ underwater observations, plankton sampling and laboratory behavior studies suggested that M. stellifera's tendency to swim was greatest during the manca larva stage, especially when brood releases coincided with new and full moons of lunar cycles. It was suggested that this behavior was responsible for larval dispersal at times of rapid population growth.
8. Two independent swimming methods were employed by M. stellifera. In one, by the concerted rotation of thoracic and third maxilliped exopodites, and in the other by the flexion of the abdomen. The former was the most efficient means of locomotion through the water.
9. In burrowing, M. stellifera used the thoracic endopodites to excavate a depression in sand, while thoracic endopodites and uropods were used to plow through sand. Laboratory and in situ underwater observations showed that M. stellifera inhabited surface sands and did not burrow to depths greater than about 1 cm.
10. Laboratory observations showed that M. stellifera is an epistrate feeder. Feeding appendages were used to gather

and hold sand grains, and, presumably, to remove and ingest food from sand grain surfaces. Substratum preference experiments indicated a choice of unaltered over treated habitat sands, and a choice of air-dried over acid-cleaned habitat sands. These results were correlated with the occurrence of micro-organisms on habitat sand grains, and it was concluded that these micro-organisms constitute M. stellifera's primary food source. Additional food sources are plant and animal detritus.

11. The sand shrimp, Crangon septemspinosus, and the flatfish, Liopsetta putnami, preyed on M. stellifera under experimental laboratory conditions. Stomach analyses showed that other flatfish species and diving sea ducks preyed on other cumacean species at neighboring beaches and in the Great Bay estuary.

12. Salinity tolerance experiments of 5 to 20 °/oo were inconclusive, but the data suggest that M. stellifera is not particularly euryhaline.

13. Thirty-two species representing five phyla constituted the macrofaunal associates of M. stellifera at Jenness Beach for four seasonal subtidal transects. Crustaceans comprised over 90% of the fauna for every season, and of these, amphipods and cumaceans were the two most abundant orders. The amphipod, Bathyporeia quoddyensis, and M. stellifera were the first and second numerically dominant species, respectively. It is proposed that nearshore subtidal sand associations of the western Atlantic boreal region, possessing physical and biological characteristics

similar to Jenness Beach, be characterized as Bathyporeia - Mancocuma associations.

14. Extrapolation of the maximum density obtained for M. stellifera at Jenness Beach gave a theoretical density estimate of 39,868/1.0 m^2, a value unsurpassed in the literature for Cumacea. Considering this theoretical estimate, the ranking of M. stellifera as second in dominance among the Jenness Beach subtidal fauna, and laboratory data concerning predation on M. stellifera, it is suggested that M. stellifera plays a significant role in the exchange of energy within the Jenness Beach ecosystem.

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